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SOME CONTRIBUTIONS OF A FIFTEEN-YEAR LOCAL STUDY OF THE NORTHERN BOBWHITE TO A KNOWLEDGE OF POPULATION PHENOMENA

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TABLE OF CONTENTS

	PAGE
INTRODUCTION	3
THE AREA	3
WEATHER BACKGROUND	6
POPULATION STATUS OF WILD HIGHER VERTEBRATES OTHER THAN BOBWHITES	6
Predators	6
"Buffers"	7
Wild Galliformes	8
SEMIANNUAL CENSUS DATA FOR THE PRAIRIE DU SAC BOBWHITE POPULATIONS	8
BOBWHITE WINTER LOSSES AND THRESHOLDS OF BASIC SECURITY	8
Dissociation of Variables	8
Emergency and Nonemergency Losses	9
Wintering Histories	9
The Threshold Concept	11
Threshold Changes	12
BOBWHITE SUMMER GAINS	12
Limitations of Summer Data	12
Inverse Ratios in Rates of Gain	13
THE QUESTION OF PHASE-LINKAGE BETWEEN RATES OF SUMMER GAIN AND NONEMERGENCY WINTER LOSSES	14
INFLUENCE OF CHANGES IN SO-CALLED LIMITING FACTORS ON THE POPULATION STATUS OF THE PRAIRIE DU SAC BOBWHITES	14
Weather and Environment	14
Predators and "Buffers"	15
Competitive Galliformes	17
The Density Factor	19
SYNCHRONY AND PERIODICITY SHOWN BY DEPRESSION PHASES OF HIGHER VERTEBRATES IN NORTH-CENTRAL UNITED STATES	21
THEORY OF DEPRESSION PHASES	28
SUMMARY	32
LITERATURE CITED	32

Museum
Zoology
Desert
6-2-49
66195
Vol 15, no 1-4

SOME CONTRIBUTIONS OF A FIFTEEN-YEAR LOCAL STUDY OF THE NORTHERN BOBWHITE TO A KNOWLEDGE OF POPULATION PHENOMENA

INTRODUCTION

This paper attempts to bring up to date certain findings from a population study of the bobwhite quail (*Colinus virginianus*) in the vicinity of Prairie du Sac, Wis., 1929-44.

The investigation is one of several involving long-term, intensive observations of this species on definite areas in Wisconsin and Iowa. Because of the accuracy and continuity of winter censuses there and the relative clearness of the ecological picture displayed by some types of "key" data, Prairie du Sac is regarded in many ways as the most informative of the areas.

Although the early studies at Prairie du Sac have been well covered in the literature, data acquired over the greater part of a decade remain to be reported. These do more than merely pyramid evidence on phenomena that were adequately understood after the first years of work. It is true, for example, that virtually as much was known about starvation in wintering bobwhites by the mid-thirties as now but a number of concepts of population mechanics have been importantly modified by evidence more recently becoming apparent.

The present paper, despite the increasing reference to many species of animals that may be noted as treatment progresses, is essentially restricted in scope to the bobwhite. Even what may appear to be outright digressions are purposely included for the bearing they have upon the main subject matter. Nevertheless, the paper also is prepared in the hope that it may take us closer to principles of populations in higher vertebrates, generally, especially as relates to automatic controls and adjustments in rates of loss and gain.

The original Prairie du Sac data, here summarized, accrue from about 1,000 man-days of field work.

The 1929-32 studies were conducted throughout the year, chiefly by me but also with the help of Albert J. Gastrow, an experienced outdoorsman, resident in the area. This was done in connection with a program established at the University of Wisconsin by the Sporting Arms and Ammunition Manufacturers' Institute and the Bureau of Biological Survey, formerly of the U. S. Department of Agriculture. Thereafter, the area's investigations with which we are concerned in this paper consisted of winter (October or November to April) censuses and observations by Gastrow and were financed through Iowa cooperation (Iowa State College and the former Iowa Fish and Game Commission, with the aid of funds contributed by J. N. ("Ding") Darling), 1932-34; Wisconsin Alumni Research Foundation and the Iowa cooperators, 1934-35; Wisconsin Alumni Research

Foundation, 1935-36; National Association of Audubon Societies, 1936-37; Thomas E. Brittingham, 1937-38; Aldo Leopold, 1938-39; Wisconsin Conservation Commission (Pittman-Robertson funds), 1939-40 and first part of 1940-41; Aldo Leopold, second part of 1940-41; Wisconsin Conservation Commission (Pittman-Robertson funds), 1941-44.

In 1933, the year following my change of residence from Wisconsin to Iowa, the 1929-32 findings on wintering of bobwhites on the Prairie du Sac and other Wisconsin areas were published (18). The Prairie du Sac studies continued under my supervision until the spring of 1935 and furnished much of the basis for a long report in 1936 (33). During later years, while continuing to examine each season's data as they became available, I made no visits to the area, and the credit for keeping the program alive should be given very largely to the efforts—sometimes personal sacrifice—of Aldo Leopold, Professor of Wildlife Management at the University of Wisconsin. From 1941 to 1943, according to our opportunities, Leopold and I worked over the data with a view toward joint publication; by 1944, however, Leopold's schedule permitted no further expenditure of time on the project, and he invited me to go ahead on my own responsibility with the preparation of the manuscript.

Not here reported are supplementary studies at Prairie du Sac, begun in 1941 by members of the staff of the Department of Wildlife Management of the University of Wisconsin. Data from these will be written up for separate publication by the persons responsible for them.

Numerous individuals and organizations other than those already mentioned have given major help, some of which will later be acknowledged in appropriate places in text or bibliography. Among others deserving thanks for their cooperation, especially in the early years, are E. D. Ochsner of Prairie du Sac and W. B. Grange, now of Babcock, Wis.

THE AREA

The 4,500 acre study area (Fig. 1) lies on the east side of the Wisconsin River, at the corner of Columbia and Dane counties, opposite the village of Prairie du Sac. It includes the 3,200 acres referred to in other publications and in addition some bordering land. It is situated in the "dairy belt" of south-central Wisconsin, and has hills partly covered by hardwoods and valleys in pasture or cultivation.

Here, the bobwhite lives on the northern edge of its established range. To the northward are found only frontier populations of this "farm game" bird, usually sparse and discontinuous, though sporadically abundant (50, p. 45).

The Prairie du Sac Area

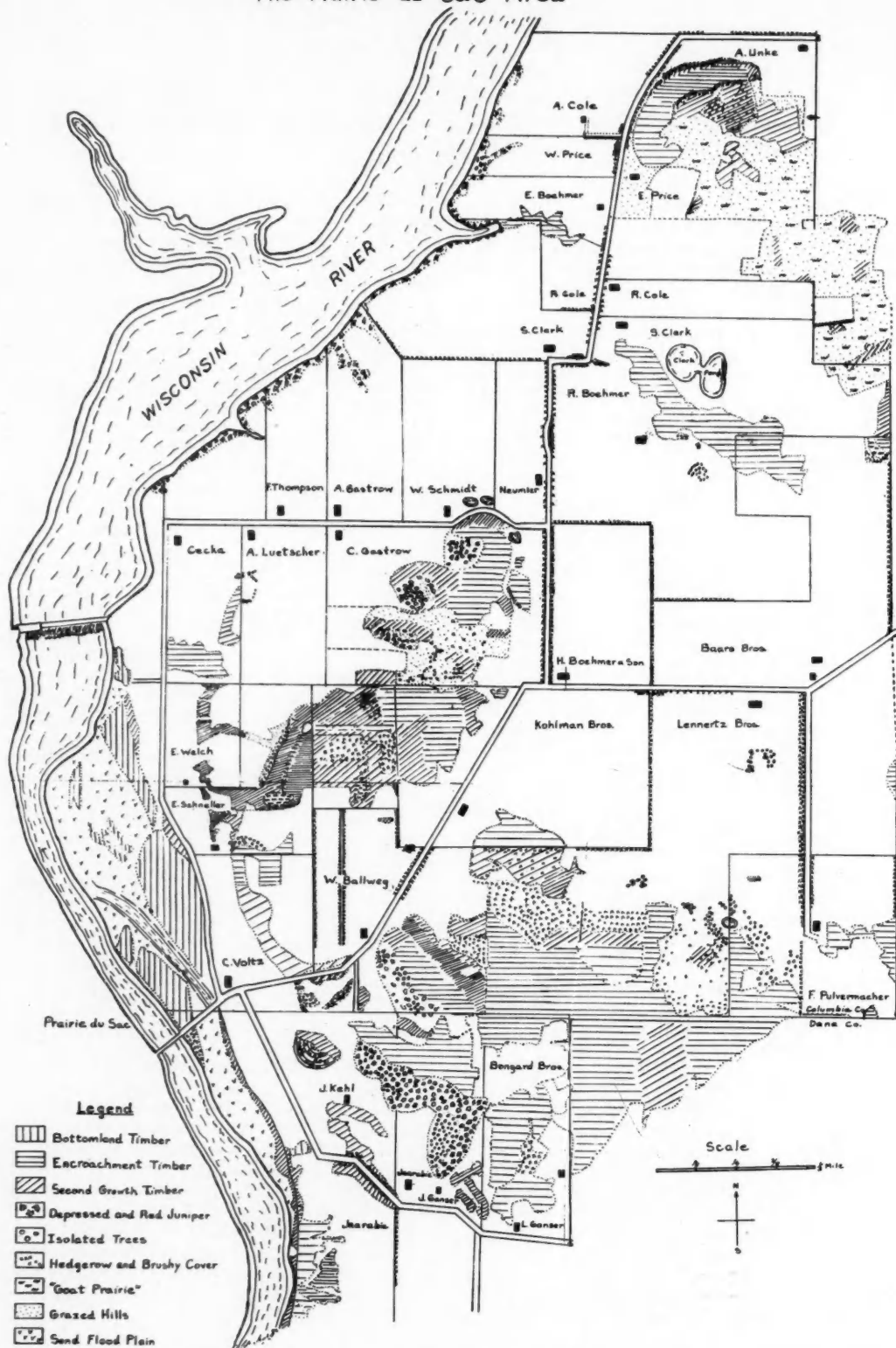


FIG. 1. Study area east of Prairie du Sac, Wis. Map drawn by H. C. Hanson for Department of Wildlife Management, University of Wisconsin.

According to the evidence I have, local farming practices did not change perceptibly during the studies. Most woodlots were pastured and some were slashed. Trees and shrubs resistant to grazing by cattle encroached on sandy tracts and steep slopes. Frequent debrushing of roadsides produced its own plant and animal successions. Professor Leopold and Cyril Kabat, a graduate student who has done much work on the area, judge, on the basis of the 1934-35 cover map (33, pp. 394-395) and the recollections of Gastrow, that cover conditions for the bobwhite have long been deteriorating.

No artificial feeding, cover improvement, control of hunting or other form of bobwhite management was attempted. Hunting seasons on this species opened during the autumns of 1932 to 1935 and, on the Dane County part of the area, again in 1942 and 1943, but negligible numbers of the local birds were shot. Hunting of rabbits and squirrels and trapping of fur-bearers was similar to that usually carried on throughout the region. There were no "anti-vermin"

campaigns; sometimes a hunter or a farmer shot a hawk or an owl. Foxes were hunted on occasion for sport or pelts. On the whole, resident wildlife was neither subject to excessive exploitation (or persecution) nor given more than passive encouragement.

For research on a species as relatively sedentary as the bobwhite, the Prairie du Sac area has many advantages. Nearly half of its periphery is bounded by a river sufficiently wide to discourage crossing by these birds at any season. On other sides, extensive tracts of habitat unfavorable for wintering bobwhites (deep woods and bare fields) help to reduce the chances of covey ranges being partly in and partly out of the area—one of the worst sources of confusion in many studies. The variables due to ingress and egress of wintering coveys are also lessened by the area's large size, as the majority of the coveys resident may engage in "normal" movements without crossing the borders. In most winters, tracking snows come often enough and last long enough to facilitate census-taking and "reading of sign."

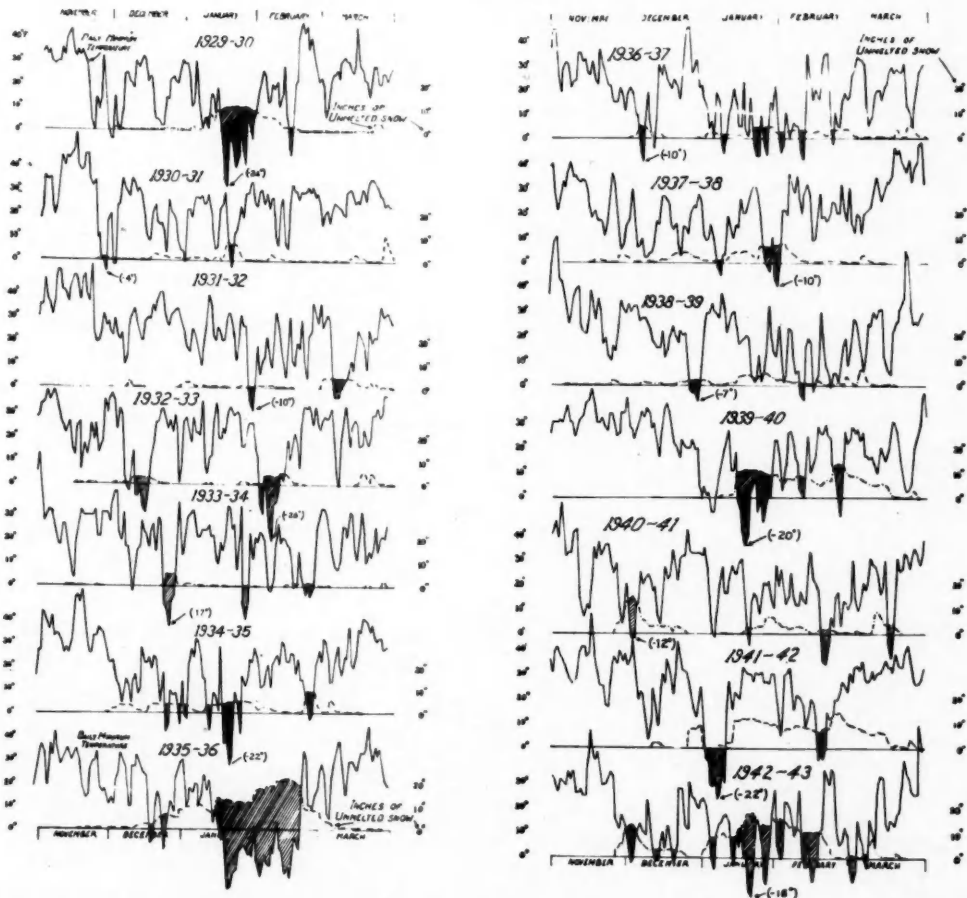


FIG. 2. Daily minimum temperatures and depths of snow on ground at Madison, Wis., winters, 1929-43. Prepared by Aldo Leopold from U. S. Weather Bureau data.

Furthermore, the area is one of those on which H. L. Stoddard had spent his early years as a naturalist. After completion of the Cooperative Quail Investigation of southeastern United States in 1929 (66), he served as Biological Survey supervisor for a number of newly initiated cooperative studies of wild gallinaeous birds, including this one of Wisconsin bobwhites. The local program at Prairie du Sac was begun upon his advice and under his excellent guidance in the field.

WEATHER BACKGROUND

No precise weather data are available from Prairie du Sac for the period of study, so we must substitute records of the U. S. Weather Bureau for Madison, which is about 20 miles southeast of the area.

Figure 2 depicts temperature and snow depths for each winter except 1943-44, with times of simultaneous cold and snow being hatched for emphasis.

Figure 3 is an extension through 1942 of Wade's (67) use of an index of drought intensity proposed by Munger (59), the base of each triangle covering a time in which no rain exceeded a twentieth of an inch per day.

Figures 2 and 3 are not claimed to register influence of weather upon the bobwhite.

As will later be shown, the winter of 1931-32, which looks mild on the chart, was terminated by a lethal emergency, and the winters of 1932-33 and 1934-35 look more similar when charted than one might expect from a far greater mortality associated with weather in 1934-35. Likewise, the mild-appearing winters, 1936-38, brought ice-storms and other ungraphed emergencies. The extremely severe winter of 1935-36 registers very well, but the "Armistice Day Blizzard" of November 11-13, 1940, looks unimpressive, although it killed many animals ordinarily weather-proof.

In Figure 3, the intensity of the 1934 drought appears far to surpass that of 1936. The latter summer does not look appreciably drier than most of the other summers, yet Wade (67, p. 560) states that "the damage done in 1936 was at least as great as in 1934."

POPULATION STATUS OF WILD HIGHER VERTEBRATES OTHER THAN BOBWHITES

It is axiomatic that the ecology of a wild animal cannot be thoroughly studied without reference to the associated biota. There are also practical limits to the scope of an investigation that can be carried on intensively by a few persons.

In this, an intensive study of the northern bobwhite, the associated species considered especially worthy of attention fell into three categories: (a) predatory species, (b) so-called buffer species, and (c) species possibly competing with the bobwhite as phylogenetically related forms.

PREDATORS

Presented in Table 1 are the available figures on winter densities of the principal large raptorial birds,

foxes, and certain small and medium-sized fur-bearers.

The number of great horned owls (*Bubo virginianus*) regularly wintering on the area varied from four to eight and averaged six, or about one per square mile. In most springs, a nest was found for each two owls, but, in 1937, 1940, and 1944, no nests were found, and it is unlikely that any were overlooked. Food habits and prey relations of the species have recently been discussed at some length (34).

The number of apparently wintering red-tailed hawks (*Buteo jamaicensis borealis*) varied from four to eight and averaged five. Field evidence indicates that these were mainly permanent residents, and, in springs when nesting data were procured, there were usually nests corresponding to every two wintering individuals listed in the notes. Failure to record nests in 1937 is laid to nonbreeding, but it is possible that late nests may have been missed.

The gray fox (*Urocyon cinereoargenteus*) has denning and ranging habits that simplify winter census work. In the early years of the study, density calculations were checked against numbers of animals known to have been taken in particular neighborhoods by hunters and trappers. Maximum winter densities of around five per square mile are suggested by the data both from Prairie du Sac and from another area near Blue Mounds, 18 miles to the south-

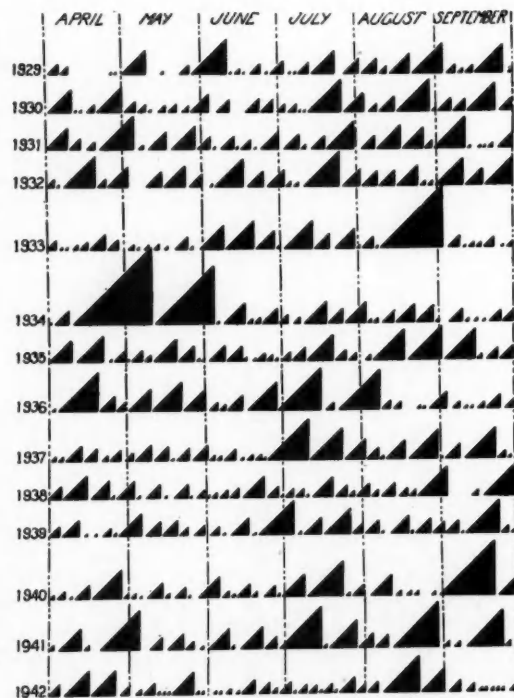


FIG. 3. Drought intensities, summers, 1929-42, plotted after Munger's method from rainfall recorded at Madison, Wis. Prepared by Aldo Leopold from U. S. Weather Bureau data.

TABLE 1. Censuses and estimates of certain predator populations, Prairie du Sac, Wis., 1930-1944.

Winter	Horned Owl Birds Nests		Red-tail Birds Nests		Gray Fox Nov. Apr.		Red Fox	Skunk	Mink (General winter estimates only)	Weasel	Raccoon	Opossum
1930-31..	4	2	4	2	16	15	0					
1931-32..	6	3	4	2	21	17	2 transients		No estimates before 1933-34			
1932-33..	6	2	?	?	27	23	2 killed					
1933-34..	4	2	6	?	18	18±	0	45	0	4	10-12	?
1934-35..	7	3	8	2-3	20±	20±	0	40	1	2	10	12
1935-36..	7	3	6	2-3	30	15	0	50	3	6	0	12
1936-37..	5	0	4	0?	30±	28±	Species present at edge of area	45	2	12	10	0
1937-38..	6	2	4	2	30±	30±	2 or 3, of which 1 was killed	75	2	6	8	?
1938-39..	5	2	4	2	10	10±	8	15	3	6	8	1
1939-40..	4	0	4	2?	5	5	5	50±	2	?	3	1+
1940-41..	8	4	4	2	6	5	4 on area most of winter; 7 killed	50	2	4	3	?
1941-42..	7	3	5	3	?	2	5 on area by Feb.; 4 others killed	75	0	6	4	12
1942-43..	6	?	6	?	2	2	13 early winter; 7 by spring	30+	2	4	7	20
1943-44..	7	0	5	?	11	8	17 on area by late Feb.; 28 others killed	70	5	5	15	10

west. The recent decline may have had a counterpart many years ago, for, after previous absence, the species was said to have reappeared locally in 1925 (50, p. 221).

Population figures for the red foxes (*Vulpes* sp.), which range beyond the area, should not be regarded as censuses, though Gastrow is an expert "still hunter" of red foxes and his opinion as to numbers should be close to the facts.

The figures on striped skunk (*Mephitis* sp.), mink (*Mustela vison*), weasels (*Mustela* spp.), raccoon (*Procyon lotor*), and opossum (*Didelphis virginiana*) are usually based upon Gastrow's winter estimates.

Not listed in Table 1, dogs (*Canis familiaris*) and house cats (*Felis domestica*) were about as abundant as they ordinarily are in midwest farming communities. Stomach contents of the few feral cats collected were similar to those of gray foxes. Gastrow estimated that there were five badgers (*Taxidea taxus*) resident in the winter of 1941-42; eight alive by the end of the winter of 1942-43; and 15 in 1943-44.

Of miscellaneous raptorial birds, barred owls (*Strix varia*) occurred regularly near the area but not often on it. Screech owls (*Otus asio*) were also to be found in some places, and there were variable populations of long-eared owls (*Asio otus wilsonianus*) and short-eared owls (*Asio flammeus*). Cooper's hawks (*Accipiter cooperii*) and marsh hawks (*Circus cyaneus hudsonius*) were often seen in summer and were irregular winter visitors. Bald eagles (*Haliaeetus leucocephalus*) wintered along the river; Gastrow has seen as many as seven in one day. Snowy owls (*Nyctea scandiaca*) and saw-whet owls (*Cryptoglaux acadica*) appeared infrequently in winter. Three goshawks (*Accipiter gentilis atricapillus*) stayed on the area for about a week in 1935-36 and another was recorded for early winter, 1943-44.

"BUFFERS"

Before 1941-42, when H. C. Hanson, a graduate student of Professor Leopold, made careful censuses of small mammals and birds (unpublished), no numerical data on "buffer" densities were obtained; great changes in populations were noted, however.

Cottontails (*Sylvilagus floridanus*) were considered "normal" for the area up to and including the winter of 1935-36. For 1936-37, Gastrow judged the cottontail population to be only about one-third "normal," and low densities were reported for other southern Wisconsin counties (53). Recovery at Prairie du Sac was visible by the winter of 1937-38; for the next two winters, numbers were again "normal"; and in 1940-41, Gastrow commented that he never before had known the rabbits to be so numerous. In 1942-43, they again were abundant; in 1943-44, much less so.

The white-tailed jackrabbit (*Lepus townsendii campestris*) has long been found on a sand prairie west of Prairie du Sac but occurrence on the area itself has been irregular.

The principal mice were meadow mice (*Microtus* spp.) and deer mice (*Peromyscus* spp.) of which the former showed much more pronounced fluctuations. It was plain that meadow mice were exceedingly abundant in 1929, 1938, and 1942, and there also was evidence (from their representations in the diets of local predators) that they may have reached another peak in 1934. The barn rat (*Rattus norvegicus*) spread into fields from farm yards in the warmer months but seemed unable to winter far away from buildings.

Populations of fox and gray squirrels (*Sciurus niger rufiventer* and *S. carolinensis*) appeared to be sparse but rather stable. Other resident sciurids included the woodchuck (*Marmota monax*), chipmunk (*Tamias striatus*), flying squirrel (*Glaucomys volans*),

and the two common ground squirrels, *Citellus tri-decemlineatus* and *C. franklini*.

WILD GALLIFORMES

Semiannual population figures for ruffed grouse (*Bonasa umbellus*) and ring-necked pheasants (*Phasianus colchicus torquatus*) are given farther on in this paper, in Figures 12 and 6, respectively. Neither grouse nor pheasant data are uniformly accurate, being for some seasons no more than estimates based upon miscellaneous "sign." The grouse may be regarded much more as true residents of the area than may the more mobile pheasants, which drifted irregularly across the land boundaries.

Judging from the annual survivors as noted in spring, the ruffed grouse populations wintered with fair security during the first 12 years at or under levels of 18 to 20 birds. In 1941-44, they varied from 30 to 38 (the spring density for 1944 was 32, not given in Fig. 12), or at levels approximately twice those for the earlier years. These grouse were legally protected throughout the study and, like the bobwhites, suffered little shooting. Unlike the bobwhites, they were not very susceptible to winter emergencies.

Large-scale pheasant stocking in Wisconsin began in 1928, but at Prairie du Sac, these exotic birds have not as yet shown any strong ascendancy—unless the 1941-42 density be so considered. A local farmer released 30 to 80 artificially propagated pheasants in August of each year since 1939.

Of other wild Galliformes, a flock of about 74 prairie chickens (*Tympanuchus cupido pinnatus*) was seen on the area in January, 1933.

SEMIANNUAL CENSUS DATA FOR THE PRAIRIE DU SAC BOBWHITE POPULATIONS

The data for the area's spring and fall populations of bobwhites, presented in Figure 4, were obtained by direct enumerations of local birds (for description of techniques, see 18, pp. 1-11; 33, pp. 310-333), which I have endeavored to sum up as for comparable times of each year.

Some trends may be detected in the gross fluctuations, but others are so obscured by variables as to be meaningless without further exposition. This is notably true with respect to winter losses after 1933-34, many of the summer gains after 1935, and the similarities the fluctuations may have with those of other species.

Readers are therefore advised not to strive overhard to draw conclusions from Figure 4 but to keep it in mind for reference as the discussion progresses.

BOBWHITE WINTER LOSSES AND THRESHOLDS OF BASIC SECURITY

DISSOCIATION OF VARIABLES

During the winters of my active participation in the field work at Prairie du Sac, emphasis was placed upon detection and analysis of mortality and

of intercovey adjustments. Fewer details were obtained thereafter, except as related to census figures, until the beginning of the supplementary studies by Professor Leopold's graduate students in 1941-42.

Prior to banding started by Kabat in 1942-43, conclusions arrived at through field observations on winter movements of Prairie du Sac bobwhites were checked mainly with the findings from earlier banding near Madison (17) and with those from Stoddard's extensive banding program in southeastern United States (66, pp. 167-182). Local movements were commonly followed with satisfaction for coveys living well inside of the traversable boundaries of the area, but the fortunes of border coveys were not always readily ascertained. Abrupt disappearance of such flocks that had been wintering without much loss was considered reasonably good evidence that they had moved out. Sometimes such coveys soon returned and sometimes the courses of those departing were traced. The area's winter egress tended to exceed its ingress, especially at the northeast corner where the birds could almost be depended upon to leave before a winter was over.

When a covey starved, the evidence was characteristic and not likely to be overlooked or misinterpreted by an experienced observer, even when complicated by killing weather and by raiding and scavenging of flesh-eaters (18, 27).

Outright losses due to weather were less easily appraised, as were the consequences of burning, close pasturing, fall plowing, and similar human activities that may often leave large tracts of land nearly foodless and coverless for bobwhites. Circumstantial evidence of declines associated with these factors was acceptable only with reservations.

Voluminous data on food habits of locally resident predatory birds and mammals—particularly horned owls, which proved to be exceptionally good indicators of vulnerability (26)—were obtained in the early years of the investigations. Much "sign" of killing or eating of bobwhites was found then and dur-

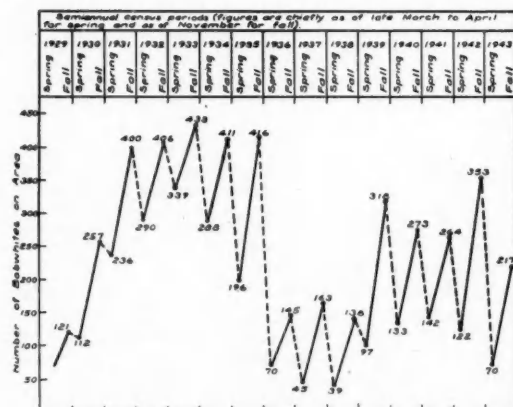


FIG. 4. Gross fluctuations, spring and fall, recorded for bobwhites at Prairie du Sac, Wis., 1929-43.

ing the last four winters. Responses of predators were correlated as much as possible with changes in availability of covey groups at times of hunger crises and of increased intraspecific friction, massing, and wandering (24, 33, 34). At its best, this was the most carefully executed part of the work, but the data are by no means of uniform quality.

Losses from accident, shooting (especially if illegal), pathology, and atypical immaturity, though difficult to record on a quantitative basis, clearly were not responsible for any extreme reductions in the bobwhite populations wintering at Prairie du Sac. Discoveries of feathers and picked bones were considered of very limited analytical significance unless contemporaneous loss trends were otherwise well defined—as by the contents of owl pellets or nests, bunched remains of covey groups at sites of melted snowdrifts, and underweight carcasses or feeble flight powers of members of starving coveys.

EMERGENCY AND NONEMERGENCY LOSSES

Emergency losses for bobwhites are those reflecting weather extremes, drastic though temporary reduction in habitability of environment, and the impacts of many of the special hazards introduced by civilized man. Losses from subhuman predators, collectively, are here considered of emergency types *only* when suffered by bobwhites made vulnerable primarily as a result of an emergency, i.e., birds weakened by hunger, crippled by shot wounds, evicted by snow or ice storms, floods, fires, etc.

Nonemergency wintering losses are broadly those suffered by populations of "normal," mature birds living free from adverse human interference in environment which, favorable or not, retains practically its full winter habitability. In other words, non-emergency losses at Prairie du Sac are of types to be expected in mild, open winters, among bobwhites that have little to contend with except their own selves and their usual kinds of enemies and competitors, hence are about the minimal losses consistent with anything to be called naturalness.

In looking over the following wintering histories the reader may avoid the confusion of possible fine-drawn distinctions by keeping a few things strictly in mind. In practice, our chief preliminary task will be to winnow out, by one means or another, the declines occurring: (a) directly through predation; (b) through population adjustments of the birds, themselves; or (c) through predation and adjustments in combination.

This done, when we have reconstructed a picture of what the histories were or probably would have been in the absence of emergencies, we should be better able to search for basic attributes of north-central bobwhite populations.

WINTERING HISTORIES

Bobwhites at Prairie du Sac were known to have been greatly reduced during the winter of 1928-29. Snow was said to have accumulated to a depth of four feet. Gastrow, before the program was organ-

ized, observed a single covey, which shrank from 30 to about six birds. The surviving population of the area was calculated on a pro rata basis to be about 22 (33, p. 422), but this figure is no longer thought to be reliable. Lacking area-wide census data, we are entitled to say of the 1928-29 survival only that it may have been as low as at any time in subsequent winters.

Starvation and associated losses were locally severe in southern Wisconsin in 1929-30, the first winter of intensive study (18). However, the Prairie du Sac population happened to have been well fed, and a survival figure of 112 of 121 birds, as of April 1, was arrived at (21, p. 112).

The winter of 1930-31 was sufficiently open to afford relief from food crises to the bobwhites of the southern Wisconsin observational areas. At Prairie du Sac, the reported survival of 236 of 257 birds (21, p. 112) indicates a loss rate differing little from that of 1929-30.

The winter of 1931-32 was similar in open-ness to that of 1930-31 until March. Then, snows brought about widespread deprivation by burying the food left on the ground. The severest emergency losses observed took place in the Wisconsin River bottom-lands southwest of Prairie du Sac. Here, 15 birds survived of a population that totalled 90 at the time of a January census and between 83 and 87 in early February (18, p. 28). On the study area east of Prairie du Sac, a 400-bird population was reduced to 290, but the losses ascribed on fair to excellent evidence to starvation were only in the vicinity of 39 (21, pp. 112-113). As the majority of the coveys had been living with slight loss from any cause for weeks prior to the lethal snowfall (18, pp. 25-27), they would in all likelihood have successfully wintered except for the emergency. Adding the 39 to the 290, we get 329, representing probable survival under nonemergency conditions.

Contrasted with the moderately light emergency losses at Prairie du Sac at the end of the 1931-32 winter, the earlier reduction from 400 to 329 comprises a substantial nonemergency loss, which for the first time in the Wisconsin investigations, occurred largely through predation upon physically "normal" bobwhites. (For data on the role of horned owls in this reduction, see 24, pp. 247 and 250, and 34, pp. 834-835, family studies 7 and 9.)

Bobwhites wintering at Prairie du Sac in 1932-33 were mainly favorably situated with respect to weather and food. A population of 406 was reduced through nonemergency losses to 339 by spring (21, p. 112), or to a level comparable with that surviving in 1931-32 up to the spring crisis. As in 1931-32, the preponderance of the mortality specifically traced was through predation upon apparently "normal" birds (19).

Nor were emergency losses considered important at Prairie du Sac in 1933-34, with the possible exception of those attributed indirectly to the debrising of roadsides by relief labor. The debrising was indeed drastic, and I estimated at the time and

Surviving 1943
Fall
21
70

on the ground that 30 to 40 birds (the equivalent of two full coveys) had been evicted without the possibility of their finding suitable quarters elsewhere in the area (33, p. 362). This number added to the survival figure of 288 actually recorded for an initial population of 433 would give a nonemergency survival close to that calculated for 1931-32 and to that realized for 1932-33. I now question that the 1933-34 evictions were quite as lethal as then thought; but whether they were or not, it is apparent that the total nonemergency decline brought the population down to around 300 birds.

The winter of 1934-35 was one of weather-linked food shortages. Much habitat was made untenable, and many birds were forced to invade covey ranges already having populations as high as were usually accommodated. A spectacular acceleration of predation—especially by horned owls—followed this massing, but range units not seriously affected by the food shortage wintered about as many birds as in the past, and the predation on these tended to cease with relief from crowding (23, pp. 563-565; 24, pp. 247-248; 33, pp. 362-364; 34, pp. 800-801 and p. 849, special phase study 13). A total of about 100 birds either left the area or died from starvation and storm. Despite reduction by spring to 196 birds from an initial 411, some 350 got along fairly well during the first half of the winter before the crisis became acute. Nonemergency losses would therefore appear about as substantial as for similar densities during the preceding three winters. We may see that a survival in excess of 300 birds—possibly 330?—could reasonably have been expected had it not been for the emergency conditions.

In 1935-36, there was a period of deep snow and some cold weather between late December and the middle of January, but, of an initial 416 birds, a fairly well-established population of at least 329 remained by midwinter. This suggests both a non-emergency decline not differing greatly from those of 1931-35 and the prospect of a comparable—300?—spring survival except in the event of lethal emergency. The emergency that did come resulted from several weeks of the severest winter weather shown by Weather Bureau records for the region. Blizzard followed blizzard, with prolonged, intense cold and much snow. One after another of the Prairie du Sac coverts was nearly or quite depopulated of bobwhites. By spring, only 70 of the birds were left alive on the area (52, p. 415).

Emergency losses in 1935-36 showed some departures from those observed in earlier years (27, 52). Typically, the bobwhites subsist on concentrated foods such as grains and the more nutritious of weed seeds and are unable to endure much fasting. They starve when heavy snowfalls cut off their food supply for a week or more at a stretch. In cold weather, the hunger-weakened are the likeliest to succumb. On rare occasions, sound birds in unsheltered places fall victim to cold, and others are imprisoned to starve or suffocate in hard-packed snowdrifts. In 1935-36, many birds died that should have been in fit enough

condition to have endured any of the weather crises between 1929-30 and 1934-35. Throughout the north-central states as well as at Prairie du Sac, bobwhites not only starved in the deep snow or died from the stress of the blizzards but also seemed to be worn down by the sustained cold.

Ice storms sealed much of the food supply of north-central bobwhites in 1936-37. By early January, a state of real emergency was manifest. The wintering population at Prairie du Sac was cut to 45 from an initial population of 145, a good part of which reduction may be attributed to easily understandable starvation. But the season's temperatures were mild, and, even before the ice storms, a decline of 25 birds had taken place. For the low population density, this was a very high rate of loss during a non-emergency period covering less than half of the winter.

Comparison of this early-season with the all-winter losses of 9 of 121 and 21 of 257 in 1929-30 and 1930-31, respectively, entitles one to ask whether the area would have wintered greatly more birds than it actually did in 1936-37 if the winter had been emergency-free—possibly about 100 instead of the 45? If such an estimate comes anywhere near the truth—and I regard it as the most defensible one I can make—then the situation in 1936-37 was quite different from that in any of the winters 1929-36.

The winter of 1936-37 had the only one of three low to moderate populations so far studied at Prairie du Sac that did not appear to be well accommodated under nonemergency conditions, and all of the five populations beginning winters with 400 birds or more either succeeded in wintering about 300 individuals or showed that they could have done so in the absence of emergencies.

The winter of 1937-38 was also mild, but a food shortage aggravated by heavy snows in late January was attended by extreme losses. The area's spring level of 39 bobwhites remaining of an initial 163 was the lowest for which we have accurate measurement. In contrast with the early, pre-crisis loss of 25 of 145 birds in 1936-37, the 1937-38 population lost only nine before the emergency period—and eight of those were lost in three ranges abandoned in late December and early January. The good survival in the majority of the coveys up to midwinter recalls 1929-31, and it would be easy to believe that, under nonemergency conditions, a much larger population than that actually entering the winter could have gotten through with low losses.

A 1938-39 decline of 41 from a fall level of 138 was recorded. Sudden losses of 13 birds in December and six birds in late winter took place in two border coveys that otherwise lost only two birds, and these 19 were judged simply to have left the area. Even after making allowance for such departure, a mainly nonemergency loss of 22 is still fairly heavy, compared with that for 1929-31 and 1937-38.

The second half of 1939-40 began with a heavy snow and a minimum temperature of 20° F. below zero. Snow and cold worked in deadly combination

for several weeks. Only 133 of an initial 318 bobwhites were reported alive on the area by spring, but 38 of those listed in the decline wintered off the area after leaving in January. The effects of a contemporaneous crisis on a 4,200-acre area near Ames, Iowa, were personally studied in detail; 46 birds of a late December population of 231 were definitely known to have died, 37 carcasses having been recovered from three starving coveys, alone (30). Up to midwinter at Prairie du Sac, most coveys maintained their numbers with little loss from any cause. At least 245 and possibly almost 290 were judged, on the basis of the covey records, to have stood a good chance of surviving had it not been for the emergency. In my opinion, the evidence favors the lower of the two figures given above, so perhaps we may suggest a nonemergency survival of about 255.

The decline to 142 from 273 birds in 1940-41 must be said to have been in part associated with unfavorable food conditions in certain covey ranges, although there wasn't much evidence of starvation except in one covey. Field notes described what could be interpreted as a generally marginal habitability of occupied quail land, unrest and local massing of birds. Predation losses were unexpectedly severe, and there was decisive evidence of something more than an ordinary emergency. Even if the starved-out covey had survived, the spring population would have been only 159. It does not seem probable that many more than the 142 actually surviving would have survived a nonemergency winter.

Save for a blizzard in early January, 1941-42 was mild. Predation again was heavy, and only 122 of an initial population of 264 bobwhites were present in spring. In this instance, emergency losses accompanying or following the blizzard had a fundamentally different significance than those characterizing, let us say, 1931-32, when a population had demonstrated its ability to live under nonemergency conditions until spring, finally to show a sharp loss from what almost might be called a freak accident. The February-March population in 1941-42 suffered so much predation during a period of no perceptible emergency that, January blizzard or not, we have no reason to think that the final survival figure would have been much changed if the winter had been entirely mild and snowless. For the density involved, this survival is low, indeed, as was the case in 1940-41.

The exact nature of the 1942-43 losses is badly obscured by undissociated variables. Some birds starved, but it was clear that outright starvation was not the primary medium of reduction. Live specimens handled by Kabat in the course of his banding study were generally in good flesh (unpublished). Heavy predation was noted by Kabat and Gastrow, and much in our interpretation must hinge upon whether that predation was or was not emergency-conditioned. Judging solely from the "paper evidence" made available to me, I would say that the losses look like emergency types, regardless of the lack of a wide-spread hunger crisis. Gastrow's journal refers to eight-foot snowdrifts, and Figure 2

shows a January and February depth of snow surpassed only by the 1935-36 accumulation for those two months. This could very well affect the habitability of many coverts.

Kabat (letter, Sept. 30, 1943) emphasizes night flushes of roosting bobwhites by red foxes, with individual birds alighting in exposed places to become sluggish from chilling and thus easily preyed upon by many predators. The consequences of such disturbances, nevertheless, would be accentuated during periods of cold and crusted snow (as were amply recorded at Prairie du Sac for January and February). It may be logically contended that even the losses of fox-flushed birds were emergency losses—at any rate to the extent that this type of loss would not be expected to occur during the 1930-31 sort of winter. Moreover, the numbers of bobwhites maintaining themselves fairly well until the January storms suggest that upwards of 275 might have survived a nonemergency winter.

Of singular openness until nearly the middle of February, 1943-44 may be classed as a nonemergency winter; nevertheless, of an initial population of 217 bobwhites, only 124 were alive on the area by spring. Predation losses again were heavy, reminding one of the winters of 1940-42.

THE THRESHOLD CONCEPT

As early as 1933, published reference was made to overpopulation of bobwhite environment at Prairie du Sac, but, to a considerable extent, my concept of overpopulation later proved to be erroneous—especially regarding the simple effects of apparent food and cover deficiencies (18, pp. 24-27).

At the end of the fourth winter, the low loss rates for 1929-31 and the similarity of the 1931-33 survivals after initially heavy populations had been cut down through nonemergency losses, in combination with like data from other areas, suggested the operation of thresholds of security, then called "carrying capacity" (21). Except in the event of emergencies, populations living below threshold values wintered with slight reduction through predation and self-adjustment. If exceeding thresholds, populations betrayed instability and pronounced vulnerability to predation until again reduced to secure levels.

Thresholds of security, in terms of numbers accommodated, tended to vary with different areas but to be maintained with reasonable constancy for specific areas, winter after winter. The effect of emergencies was to suspend the operation of thresholds—sometimes to the point of making entire populations insecure—but, within limits, a great deal in the nature of environmental change was known to occur without appreciably modifying threshold values. Observed differences in kinds and numbers of predators and "buffers" seemingly were not reflected in changed security of wintering bobwhites.

Data at hand from all north-central sources by the end of the sixth winter chiefly confirmed the trends that were apparent by the end of the fourth and further amplified the threshold concept (33). The

importance of obtaining population figures from complete covey ranges and sizable land units was partly recognized. Distinctions were made between "key" habitats and combinations of food and cover and those having no unique significance despite more or less regular use by bobwhites. Such interpretations of threshold phenomena as were advanced did not ignore psychological factors but emphasized the possibilities of a given threshold being primarily a property of the environment.

In retrospect, I think that for many years I was seriously misled in my attempts to analyze threshold phenomena by the evidences of year-to-year constancy in threshold values shown by the eight territorial subdivisions mapped for the Prairie du Sac area on pp. 394-395 of the six-year report (33). This apparent constancy for the designated land units continued for at least one winter—1935-36—after my personal participation in the field work had ceased. From then on, the constancy seems largely to have been lost for units much smaller than the total area.

It may be said, in short, that former territorial units have been so thoroughly merged and repartitioned since 1936-37 that many of their boundaries, as originally observed, have lost all validity, and the question of whether or not subdivisions of the area display year-to-year constancy in threshold values does not currently appear to be of more than very limited significance. Undoubtedly, the entire Prairie du Sac area shows a greater constancy in threshold values than do its constituent parts.

THRESHOLD CHANGES

From the early winter densities and the calculated nonemergency survivals that are tabulated in Figure 5, it may be judged that about the same basic threshold was operative not only for 1931-35, the last four winters for which data were published, but also very probably for 1935-36, the winter of greatest emergency, and for the low-density winters of 1929-31.

The calculated nonemergency survival of perhaps 100 and the high rate of nonemergency loss for a low-density population in 1936-37 may be construed as reflecting a lowered if not collapsed threshold of security for the area's bobwhites. The possible connection between this and periodic depression of other species in the north-central region will be taken up later.

The nonemergency loss rate for 1937-38 is so comparable with those for 1929-31, when initial populations were likewise below 300, that one might well believe the old threshold to have been again operative.

For 1938-39, the nonemergency rate is higher than would ordinarily be expected under the old high—a 300 to 330-bird—threshold, but it is not utterly excessive for a high threshold. Security, as from predation, is rarely absolute, and loss rates up to 6% per 90 days have been considered nothing unusual for recognizably secure wintering populations (33, p. 375). As will be brought out, however, the high rate for 1938-39 fits in with other evidence pointing to a suspended or depressed threshold.

The 245 to 290 bobwhites calculated to have had a good chance of surviving under nonemergency conditions in 1939-40 could be considered evidence for a threshold restored to about the 1931-36 level. A 290 survival would mean a 9% loss, which would fall on the curve outlined by the 1929-36 and 1937-38 data (lower center, Fig. 5). But, objectively regarded, a nonemergency survival closer to 245 than to 290 seems more in keeping with the field evidence. The selected figure of about 255 gives a loss rate of 20%, which is high for the curve, though still seeming to reflect a substantial basic security.

Survivals for 1940-42 offered the first really clear challenge to previously held ideas of year-to-year constancy in threshold values. Despite the questions as to the degree that the area's threshold was truly suspended or depressed in 1936-37 and the difficulties of appraising the loss rates for 1938-40, the data certainly show that something was different with respect to thresholds in 1940-42.

Complicated though they are by unknowns, the 1942-43 data revealed far too many bobwhites alive by midwinter to support any thesis to the effect that the poor actual survival merely reflected a continuation of the 1940-42 phenomena. In my judgment, the loss rate under nonemergency conditions would have been only a little above the 1929-36 and 1937-38 curve.

Lastly, for 1943-44, the status of the area's threshold apparently had reverted to about that for 1940-42.

From the nonemergency loss rates for 1938-39, 1940-42, and 1943-44, may we suspect the operation of a second basic threshold not much above 100 birds?

Further discussion of threshold phenomena may well be postponed until more evidence has been presented.

BOBWHITE SUMMER GAINS

LIMITATIONS OF SUMMER DATA

It is not implied that the increase of bobwhites on an area from spring to fall is exclusively or even largely the result of breeding of the birds present in the spring or that an individual bobwhite recorded at the time of the last winter or early spring census will necessarily remain on the area to breed. The months from late spring to early fall include, as well as the annual reproductive span of the bobwhite, periods of extensive readjustment in social groups, involving widely separated coverts and areas often to be reckoned in terms of square miles (11; 17; 33, p. 92; 66, pp. 169-182).

The quality of data obtained in warm weather studies of north-central bobwhites must be admitted to be greatly inferior to that for the winter records. Evidences of mortality and other "sign" persisted only briefly; visibility was poor in the dense ground cover; and the birds, old and young, were practically impossible to keep track of on a quantitative scale sufficient to permit bonafide week-to-week population studies. Careful summer work during the first three

Winter survivals and loss rates of wild Galliformes (other than grouse) at Prairie du Sac, Wis., as actually occurring and as calculated for nonemergency conditions. (See text for comments).										
Winter		Early winter density	Density by spring	Percent winter loss, all causes	Calculated survival under nonemergency conditions	Percent winter loss calculated for nonemergency conditions		Early winter density	Calculated survival under nonemergency condition	Percent winter loss calculated for nonemergency conditions
1929-30	Bobwhite, only	121	112	7%	112	7%	Bobwhite and pheasant, collectively	121	112	7%
1930-31		257	236	8%	236	8%		257	236	8%
1931-32		400	290	28%	329	18%		400	329	18%
1932-33		406	339	17%	339	17%		406	339	17%
1933-34		433	268	33%	300?	31%?		433	302?	30%?
1934-35		411	196	52%	330?	20%?		413	332?	20%?
1935-36		416	70	63%	300?	28%?		419	303?	28%?
1936-37		145	45	69%	100?	31%?		153	106?	31%?
1937-38		163	39	76%	150?	8%?		172	159?	8%?
1938-39		138	97	30%	116	16%		153	120	22%
1939-40		315	133	53%	255?	20%?		318	258?	19%?
1940-41		273	142	48%	142?	48%?		283	148?	48%?
1941-42		264	122	54%	122	54%		304	152	50%
1942-43		353	70	80%	275+?	22% or less?		363?	283+?	26% or less?
1943-44		217	124	43%	124	43%		231	131	43%

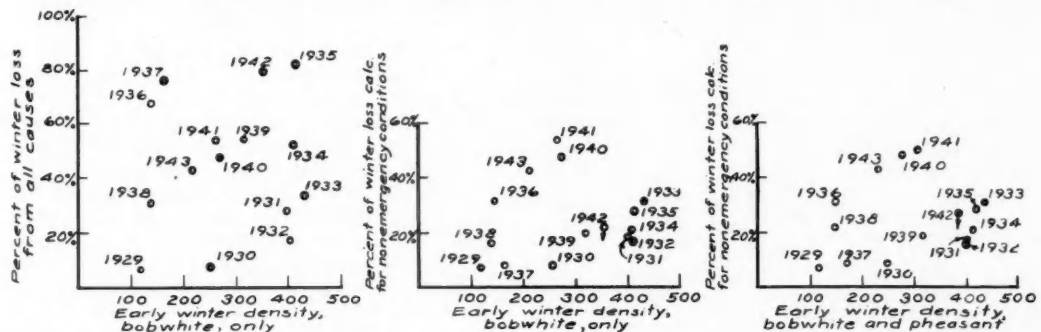


FIG. 5. Rates of loss of wintering bobwhites and ring-necked pheasants in relation to density, Prairie du Sac, Wis., 1929-44.

years in southern Wisconsin yielded scarcely passable data on nesting losses of bobwhites (20); feeding trends of, and preying upon bobwhites by, certain predators, notably horned owls (34); and fragmentary information on mortality and behavior of juvenile bobwhites. After termination of the all-year field work at Prairie du Sac in 1932, the rate of population gain by fall (checked by general observations in others parts of the region) constituted nearly the sole criterion of reproductive success.

Our summer picture is therefore all but lacking in detail, being represented rather literally by not much except the frame. But the spring and fall census data comprising the frame are of good quality and, whatever else may be said of them, afford us something definite enough to grasp. Considering nothing except the census data as they have come to hand, year after year, we are not obliged to make any assumptions whatever as to what the area's bobwhites did or did not do in the intervening months. The data are legitimately usable for analytical purposes to the extent that they show significant trends.

INVERSE RATIOS IN RATES OF GAIN

Summer gains, as shown by numerical differences between spring and fall populations in Figure 4, look highly variable; but, as plotted in percentages in the upper left of Figure 6, they reveal certain patterns.

By the fall of 1932, it had been noted that summer gains tended to be in inverse ratio to spring densities

(21, pp. 124-125), and this inverse relationship was better defined by the fall of 1935 (33, p. 422). At the time of this writing (spring, 1944), the percentages of gain in relation to spring densities for 13 of 14 summers at Prairie du Sac fall pretty well in two curves.

The principal curve, defined by the rates of gain for eight of the 14 summers (1931-35, 1937, 1939, and 1942) is a reverse sigmoid, and, as long as spring to fall rates of gain in bobwhite numbers conform to it, the fall populations should be fairly well predictable from spring densities even before the start of actual breeding.

For such years, we may ordinarily expect Prairie du Sac spring densities of about 40 birds to be followed by fall densities of about 140; spring densities of about 100, by fall densities of about 325; spring densities of about 200, by fall densities of about 400; spring densities approaching 340, by fall densities approaching 440. Stated otherwise, if the fall populations with which we are here concerned were made up only of evenly paired spring residents and their progeny—which, of course, we know is not true—the average numbers of young raised by fall per pair would be about five from a 20-pair spring level; more than four young from a 50-pair level; about two young from a 100-pair level; and not much more than one-half young from the highest observed level of about 170 pairs.

The second curve is too imperfectly defined by the

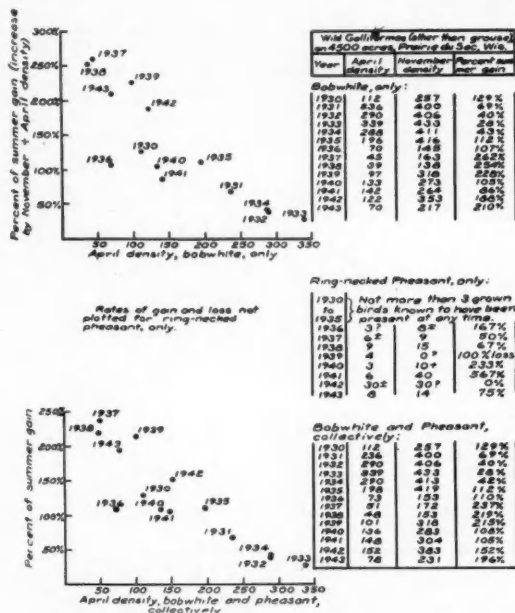


FIG. 6. Rates of gain of bobwhites and ring-necked pheasants in relation to density, Prairie du Sac, Wis., spring to fall, 1930-43.

gains for 1930, 1938, 1940-41, and 1943 to warrant many comments, particularly as concerns any possible lower asymptote that it may have. So far as it goes, it seems to reflect inverse ratios to spring densities somewhat after the manner of the first curve though on a different level of increase.

Conformation of 13 of the 14 rates of summer gain at Prairie du Sac to one or the other of two density-determined patterns has not been noticeably influenced by emergencies. In southern Iowa, a drought occurred in 1934 that was of such intensity and long duration that it virtually brought about desert conditions in local areas, and this was accompanied by summer declines in bobwhite populations (22). In other parts of the north-central bobwhite range observed during the summer and fall of that year, including southern Wisconsin, the drought seemed less severe than in southern Iowa and more within the toleration limits of the species.

The drought summer of 1936 was one of decidedly low rates of gain in relation to spring densities at Prairie du Sac as well as elsewhere in the region, but, as will be shown, drought would appear to have figured less importantly than what we, for want of understanding and a better term, must still call periodic depression.

THE QUESTION OF PHASE-LINKAGE BETWEEN RATES OF SUMMER GAIN AND NONEMERGENCY WINTER LOSSES

Let us again look at the rates of nonemergency winter losses and rates of summer gains of the

Prairie du Sac bobwhites in the lower center of Figure 5 and the upper left of Figure 6.

First, it may be perceived that, for the density levels involved, the lowest rate of summer gain—that of 1936—was followed by the highest calculated rate of nonemergency winter loss. Then, three summers—1940, 1941, and 1943—of gains depressed below the main eight-summer curve were followed by distinctly high rates of nonemergency winter loss. A similar thing seemed to have occurred in 1938, but the densities concerned were sufficiently low to make departures from the “normal” gain and loss curves hard to judge.

The slightly elevated (compared with the curve for 1929-36 and 1937-38) rates of nonemergency loss calculated for the winters of 1939-40 and 1942-43 do not follow summers for which rates of gain were depressed below the main curve. They do precede summers of depressed gains.

Of all of the data points falling outside of the two “normal” curves for rates of nonemergency winter loss and summer gain, that representing summer gain for 1930 is the only one standing by itself.

More groundwork will have to be laid before treatment of the present subject may be advantageously concluded in this paper. Meanwhile, the reader may be left with the thought that rates of summer gain and nonemergency winter loss perhaps do run in some sort of phase.

INFLUENCE OF CHANGES IN SO-CALLED LIMITING FACTORS ON THE POPULA- TION STATUS OF THE PRAIRIE DU SAC BOBWHITES

The “limiting factors” listed in publications on the natural history, ecology, or management of a wild animal usually include extremes of weather; availability of food, cover, and water; various aspects of predation (or of parasitism); and competitive relationships.

Much of the treatment of these factors in the literature is extremely hard to appraise, and a reader may have justifiable doubts as to what is desirably standardized or merely stereotyped, whether an author's statements reflect critical thinking or indoctrination, self-acquired or otherwise. Acknowledgment of some of these deficiencies in my own past writings should not make it less in order for me here to review the question of what really did limit bobwhite populations at Prairie du Sac.

WEATHER AND ENVIRONMENT

There can be no doubt that weather emergencies (notably those manifested by winter starvation) may have influence on population levels of the bobwhite in northern parts of its geographic range. These emergencies, however, show much variability, both in severity and time of onset. Their effects upon local bobwhites do not correspond closely to any natural rhythm that I can detect.

The possible influence of year-to-year variations in food, cover, and water on the Prairie du Sac bob-

whites has received a vast amount of attention without yielding much except negative information. Unquestionably, environmental changes have resulted from land-use practices in the course of the 15-year study, and we should not lose sight of the cover deterioration previously mentioned to have been noted by Leopold and Kabat.

For all of the local consequences of roadside debrushing, burning, fall plowing, removal of corn shocks, etc., recorded during investigations of the northern bobwhite, I do not think that the depressed rates of summer gain and the depressed winter thresholds at Prairie du Sac since 1936 may correctly be laid to environmental impoverishment.

The drought of 1936 had its effects on food and ground cover, but, from a short visit made in early winter 1936-37, I would say that conditions did not look appreciably worse than they had in 1931, when rates of summer gain and nonemergency winter loss had followed the patterns defined by the curves for the "normal" years. The 1940-44 data might be construed as reflecting general deterioration of the physical environment were it not for contrary evidence furnished by the summer gain for 1942 and the winter survival up to the beginning of the storm period in January, 1943. And the somewhat depressed rate of summer gain for 1938 and the elevated rate of nonemergency winter loss for 1938-39—coming as they did between the "normal" gains and losses of the summer of 1937, the winter of 1937-38, and the summer of 1939—do not look like early evidence of any permanent change in basic habitability of the Prairie du Sac environment.

Before we here strain to reconcile what is not necessarily reconcilable, let us consider some other things.

PREDATORS AND "BUFFERS"

The reader, checking back on Table 1, will find no figures on predator densities for 1929-30, for the reason that predators were not then studied on all of what was later established as the Prairie du Sac observational area. For the central three square miles, on which most of the work was done in 1929-30, the regularly active predators, "as nearly as could be determined, were one or two horned owls, at least one barred owl, several screech owls, 3 redtails, and a rather sparse population of grey foxes and weasels" (18, p. 22). This suggests that the whole area had, except for fewer foxes and more small owls, a predator population in that winter not differing greatly from that of 1930-31.

Practically any species of raptorial bird and carnivorous mammal listed in this paper may be expected to do more or less preying upon the bobwhite under conditions favoring predation. Of all of these, the horned owl, Cooper's hawk, house cat, and the two foxes were the species to which by far the greater proportion of the actual killing must be charged—to the horned owl possibly more than to all of the others together (24, p. 245). The striped skunk is well known as an egg-eater, and foxes and cats

would be likely predators upon incubating and immature bobwhites. Among the rodents, the ground squirrels, from studies elsewhere (45), may be regarded with suspicion as enemies of eggs and young.

In view of the numerically undetermined, but not noticeably changing, year-to-year status of house cats and ground squirrels, and the irregularity with which Cooper's hawks visited or lived in the area, one problem is to find whether there is a correlation between basic population phenomena of the Prairie du Sac bobwhites and changes in densities of the local horned owls, foxes, and skunks.

Another is the possibility of fluctuations in "buffer" populations influencing the status of the bobwhites. Cottontails and meadow mice were the most important "buffers" showing pronounced changes in numbers.

The lightness of the nonemergency loss rate for the winter of 1929-30 might at first glance look consistent with conventional views on bobwhite-predator-"buffer" relationships. The predator population was rather low, the meadow mouse population was high, and the cottontail population was about "average."

But the 1930-31 rate for a higher bobwhite population was nearly the same as in 1929-30. Though the horned owl and cottontail populations were evidently similar in 1930-31 to what they had been in 1929-30, the meadow mouse "peak" had collapsed months before the winter of 1930-31, and the gray fox population had risen to a moderate level by 1930-31. Cooper's hawks in 1930-31 were unusually persistent in their harassment of bobwhite coveys (18, pp. 22-24).

In 1931-32 and 1932-33, we see similar rates of nonemergency winter losses from similar bobwhite densities. The populations of horned owls and cottontails were also similar, but those of gray foxes and meadow mice were higher in 1932-33 than in 1931-32.

A higher initial density of bobwhites suffered a higher rate of nonemergency loss in 1933-34. The winter was one of fewer horned owls and gray foxes than 1932-33, about the same density of cottontails, and a population of meadow mice apparently approaching another peak.

Nonemergency losses of bobwhites were evidently nearly as great in the winters of 1934-35 and 1935-36 as in 1933-34, from nearly as high initial densities. The horned owl populations for 1934-36 were the largest thus far recorded, being almost twice as high as in 1933-34. Gray fox densities were somewhat higher than in 1933-34; there was no known pronounced change in the cottontails; and meadow mice may have reached a peak in 1934 and fallen off later. A brief visitation by goshawks was not known to have changed any trends in the bobwhite data.

Now we come to the sharply increased loss rate for 1936-37, for a low-density bobwhite population. The horned owl population was lower than in 1934-36, and the adults had no young in nests by late winter and spring. Gray foxes had virtually reached

their highest level for the area. Cottontails obviously had declined and meadow mice were probably present in moderate numbers, being on the way to their next abundance peak in 1938.

For all of the nonbreeding of the horned owls, it might be argued that the predator population of 1936-37 was still high enough with respect to available "buffers" to be forced more to seek other prey, such as bobwhites; but, in 1937-38, when cottontails were still low (though meadow mice were nearing another peak), another very high gray fox population and a horned owl population once again "normal" took only about the same relative toll as much smaller numbers of predators having much more available food had taken from the lower bobwhite population of 1929-30.

The winter of 1938-39, when the nonemergency loss rate for bobwhites was rather high for their density level, was one of meadow mouse abundance and "normal" numbers of cottontails and of what might be called an ordinary horned owl population. It was also marked by sharply lowered gray fox densities and by the largest number of red foxes observed on the area in the course of the study up to that time.

Despite lack of certainty as to the numerical value of the nonemergency loss for the winter of 1939-40, my feeling is that it was fairly high for the initial population level of the bobwhites. This, however, is correlated with no differences in numbers of predators or buffers that I can see. It is true that meadow mice had presumably declined following their 1938 peak, but cottontails were again "normal" and about to begin an ascendancy. Horned owls and both species of foxes were less numerous than they had been the previous winter.

The winters of 1940-41 and 1941-42, with their similar, moderate-density populations of bobwhites, showed high rates of nonemergency losses. Cottontails were exceedingly abundant both in 1940-41 and 1941-42, and meadow mice again reached peak numbers in 1942. The 1940-41 population of horned owls was the heaviest of the entire period of study and, in 1941-42, it was still as high as it had been in the previous winters of abundance, 1934-36. Gray fox densities were about the same in 1940-41 as in 1939-40, but this species had almost disappeared from the area by 1941-42. Red fox densities remained about the same in 1940-41 and 1941-42. The predator-prey picture for 1940-41 shows a generally higher level of bobwhite enemies and a lower level of "buffers" than for 1941-42, yet the rate of predation upon similar densities of bobwhites was, if anything, higher in 1941-42.

Regardless of questions remaining unsettled as to how much the severe wintering losses for 1942-43 were emergency or nonemergency in type, we know that there was a great deal of predation upon a fairly heavy bobwhite population. The meadow mouse population was high, as was that of cottontails, though the latter were not as abundant as they had been in the preceding two winters. Horned owls were present in "average" numbers; gray foxes

were barely represented; and red foxes were more abundant than in any previous year of the program. The association of red fox activities emphasized by Kabat might very well represent an intensification of predator pressure of a sort not observed in earlier years. On the other hand, the night flushing by gray foxes described (18, p. 28) for 1931-32—one of the winters of heavy bobwhite densities and high non-emergency survival—would not appear so dissimilar to that of the reds in 1942-43.

The winter of 1943-44 was remarkable for its fox densities. Grays were back about to their 1938-39 level, and the numbers of reds actually killed during the winter surpassed all records for any area of like size of which I know. It seems within reason that upwards of 40 foxes may have ranged over some part of the 4,500-acre tract during particular nights. Horned owls, too, were abundant, as were miscellaneous carnivores. Cottontails and meadow mice had decreased, which, with the above, would appear ideally to fulfill the conventionally accepted requirements for heavy bobwhite losses from predation.

Heavy predation in fact took place, and the possibility is not disproved that so many active and hungry flesh-eaters, by their predacious weight alone, may have forced the wintering population of bobwhites below otherwise operative thresholds of security. Nevertheless, the resemblance of the 1943-44 losses to those of 1940-42 is too great to make wholly convincing any sweeping explanations in terms of increased populations of predators and decreased populations of "buffers."

Rates of gain of the Prairie du Sac bobwhites conformed to the "normal" curve for eight of 14 summers, despite some quite pronounced differences in status of skunks and foxes, as well as of other predators. Of these "conforming" summers, 1937 was one of high skunk densities, and the summers of 1931 to 1935 and that of 1937 evidently had substantial to very high densities of gray foxes. Meadow mouse populations were low about 1935 and 1939 and cottontails were still low in 1937. The predator and "buffer" populations were probably as much out of theoretical balance in 1937 as in any summer of "normal" bobwhite recovery at Prairie du Sac.

In 1936, the year of most severely depressed summer gains for bobwhites, Prairie du Sac skunks were less abundant than in "normal" 1937; gray foxes were at a high level in 1936 but no higher than in 1937; "buffers" admittedly were present in diminished numbers in 1936, but their status by 1937 can hardly be thought to have improved so much as to explain the differences between the bobwhite gains of the two summers.

There is likewise nothing about the known predator and "buffer" situations for 1940 and 1941 to suggest a connection with the depressed gains of the bobwhites. Skunks were abundant in 1941 (about as in "normal" 1937); gray foxes were low in 1940 and still lower in 1941; red foxes were fairly numerous in 1940 and 1941, yet were more abundant in 1942, a year of "normal" bobwhite gain.

If we may judge from the fall and early winter densities, the skunks and the gray and red foxes collectively must have reached, in the summer of 1943, their greatest abundance during the Prairie du Sac studies. At the same time, "buffer" densities were at least fairly low. The depressed rate of gain of the bobwhites for this year may be said to coincide with a state of predator-prey unbalance, but the unbalance does not look any worse than it did for "normal" 1937. Even if the predators did depress the bobwhite gain for 1943, the rate does not fall much short of the "normal" curve. More likely, in my estimation, the rate of gain simply conformed to the second curve, that already outlined by the gains for 1930, 1938, and 1940-41.

The lack of connection between rates of nonemergency winter loss and summer gain and observed differences in populations of predators and "buffers" has seemed to hold pretty well for areas other than Prairie du Sac in the north-central region (29, 33). It denotes much variability in details of mortality, reproduction, and movement of the bobwhites being cancelled out in net effect by the bobwhite's own density factor, in particular. Many of the supposed advantages of favorable breeding seasons or decreased losses from enemies fail to count in the end, as do, in their turn, many of the disadvantages of unfavorable breeding seasons or of increased losses from enemies.

Thus are exemplified the intercompensatory trends in population phenomena of higher vertebrates that have been becoming more and more apparent (31, 32). How widely they apply to the higher vertebrates generally or even to bobwhites over the occupied range of that species is quite undetermined. Less flexibility in bobwhite-predator-"buffer" relationships may exist in southeastern United States, where fewer alternatives of action seem to be open to predators at times of failure of their main staple food, the cotton rat (*Sigmodon hispidus*) (35).

Known losses of free-living bobwhites from parasites and diseases at Prairie du Sac and elsewhere in the region have been so negligible, and the references to them so scattered in the literature, that the subject may here be dismissed with little additional comment. Let it only be pointed out that ordinary variations in losses through these agencies could be expected to fall into intercompensatory categories and to tend to be counterbalanced, when relatively high, by lowered losses through other agencies, and *vice versa*. A sweepingly lethal epizootic, if one occurred, would be another thing, logically classifiable as an emergency type of destruction, along with those resulting from hunger crises and storms.

COMPETITIVE GALLIFORMES

It has long been clear that the density factor had a very important role in governing population phenomena of the northern bobwhite. But how broad should be our concept of density factor?—relating to bobwhites alone or to bobwhites plus what else?

The Prairie du Sac bobwhites could hardly have been subject to severely effective interspecific com-

petition from wild animals or the basic patterns in their rates of gain and nonemergency loss would not have been so well maintained. This does not prove, however, that the patterns were totally uninfluenced by interspecific competition.

Among the faunal groups sharing the bobwhite's geographic range in the north-central region, other wild Galliformes might on general grounds be suspected of being the closest competitors. These include the native grouse and certain introduced game birds.

Existing information does not tell us much about interspecific competition in native Galliformes. It seems rather to be expected that such competition might, after a long span of racial adjustment, show less pronounced aspects than competition between native and recently introduced species having overlapping local ranges or territories. We have in native Galliformes, prairie chickens and sharp-tailed grouse (*Pediocetes phasianellus*) replacing one another in central Wisconsin counties as land is placed under cultivation or reverts, and further possible competitive relations between sharp-tails and ruffed grouse as reversion of former agricultural lands may progress; but the picture is so dominated by plant succession as to make interspecific relations of these grouse seem quite secondary (40).

It should not be thought that significant competition, when occurring, must conform to popular ideas of one species eating the other's food, destroying the other's eggs or young, or driving out the other by attack.

Ruffed grouse were not regarded as real competitors of the bobwhites at Prairie du Sac. During most years, at any rate, the grouse were fairly well segregated in types of habitat rarely visited by bobwhites. During the years of unusually high grouse populations, 1941-44 (see lower Figure 12), the grouse appeared in, and disappeared from, places in which they hadn't been seen for many years; and one would think that, if they had depressive influence on the bobwhites, it would have been at that time. However, the summer of probably the highest actual grouse density, 1942, was one for which the rate of gain of the bobwhite fell very close to the line for the "normal" curve (Figure 6, upper left).

Figure 7 presents largely unpublished data on bobwhite and prairie chicken populations of an area near Hunt City, Ill., furnished through the courtesy of Dr. R. E. Yeatter of the Illinois State Natural History Survey.

Considering the bobwhite data alone, we may see rates of summer gain that are depressed in 1936 and 1937 but otherwise show what looks like typical inverse ratios. Whatever may be the meaning of the irregularities of the prairie chicken gains, if the prairie chickens and bobwhites were mutual depressants, the latter species surely did not find itself at any overwhelming disadvantages as long as its own gains reflected primarily its own densities rather than those of the chickens, even for the summer of 1939

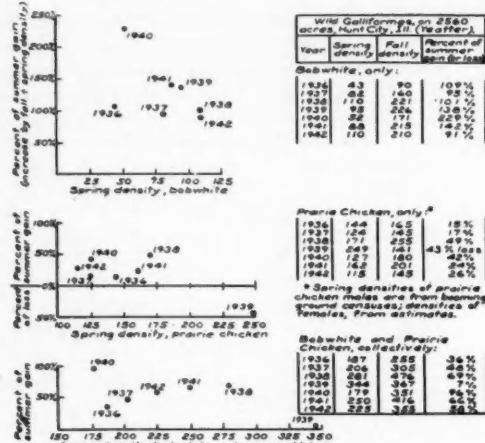


FIG. 7. Rates of gain (or loss) of bobwhites and prairie chickens in relation to density, Hunt City, Ill., spring to fall, 1936-42. Data furnished by R. E. Yeater.

following the highest spring density of the chickens.

Ignoring the variable introduced by human hunting of bobwhites for sport at Hunt City, we might judge that the survival figures for all except the emergency winters of 1935-36 and 1939-40 would suggest threshold values between 90 and 110, or in vicinity of 100. The two winters of heaviest densities of chickens—1938-39 and 1941-42—were winters of substantial reduction of bobwhites, but the survivals of 95 and 110 birds of the latter species are sufficiently close to the estimated threshold to argue against very much depression resulting from the presence of the chickens.

Preliminary to our consideration of competition between the bobwhite and the introduced ring-necked pheasant at Prairie du Sac, it may be explained that the evidence from elsewhere in the north-central region indicates that wintering bobwhites avoid coverts having many pheasants much as they do places overpopulated with their own kind. Thresholds of security tend to retain their numerical uniformity for given areas but the thresholds apply to mixed populations of bobwhites and pheasants rather than to bobwhites, alone (29, pp. 96-97). The end result of this sort of competition may then be, within limits, the exotic pheasants wintering at the expense of the native bobwhites, essentially bird for bird.

Especially because of the greater mobility and irregularity in habits of the pheasants, the density figures in my possession may often be only approximate or may be accurate only for certain times of the winter, thus necessitating careful estimating for other times. Passably satisfactory data on cold weather pheasant densities are at hand for two long-studied areas besides Prairie du Sac that have mixed bobwhite and pheasant populations (Figures 8 and 9). Unfortunately, for both areas, there are too many undissociated variables in the winter losses of the bobwhites themselves to justify attempts to plot non-

emergency loss rates. The analytical importance of reasonably accurate dissociation is well illustrated by the lower left of Figure 5, in which gross winter loss rates at Prairie du Sac give more of the appearance of a buckshot target than of any meaningful curves.

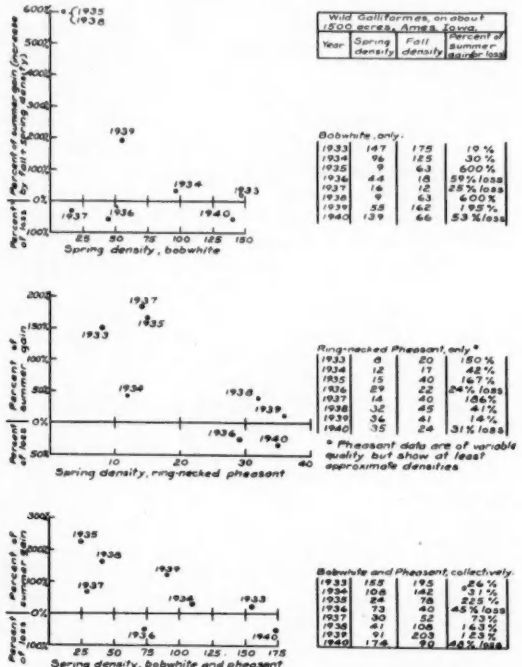


FIG. 8. Rates of gain (or loss) of bobwhites and ring-necked pheasants in relation to density, Ames, Iowa, spring to fall, 1933-40. The 1500-acre area has been described in the literature as two areas, but, for purposes of this paper, these may be regarded as a unit.

For Prairie du Sac, the nonemergency losses of bobwhites plus pheasant losses define, in combination, smoother curves than do rates of nonemergency losses of bobwhites, alone (lower right, Figure 5).

In the latter, the nonemergency loss rate beginning in the fall of 1936 still remains high for the total population of bobwhites and pheasants; but its actual numerical value is sufficiently uncertain so that we cannot be absolutely sure that it does not have affinities with the 1938-1940-1941-1943 group, which seems to define a part near the upper asymptote of a sigmoid curve. The curve defined by the nonemergency loss rates beginning in the "normal" falls of 1929-35 and 1937 also would seem to define, for one thing, part of a sigmoid, only in this case a lower asymptote. The rates for 1939 and 1942 give us "off" points, like those for the nonemergency losses of bobwhites, alone.

The rates of summer gain of the combined Galliformes at Ames conform more to definite patterns than do the rates for one component species or the

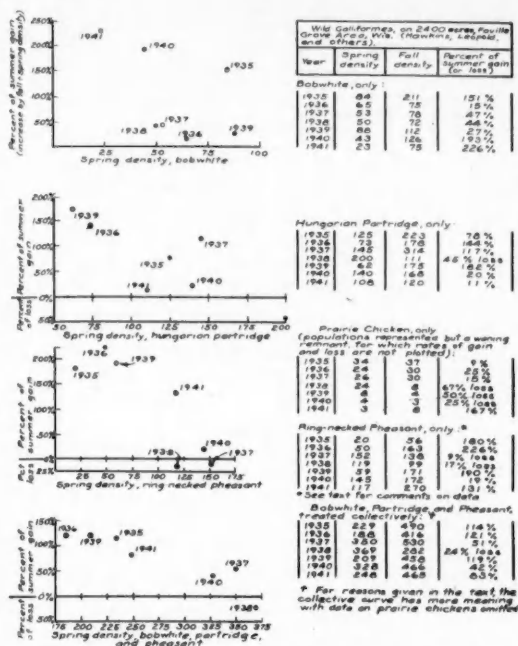


FIG. 9. Rates of gain (or loss) of bobwhites, Hungarian partridges, prairie chickens, and ring-necked pheasants in relation to density, Faville Grove area, Wis., spring to fall, 1935-41. Data furnished by Department of Wildlife Management, University of Wisconsin.

other (compare lower left, Figure 8, with upper left and left center). The loss for 1936 and the strongly depressed rate for 1937 are thought to have periodic connection. These exceptions notwithstanding, the alignment of the percentages of summer gain (or loss) leaves an impression of agreement with the principle of inverse ratios and of a substantial degree of mutual depression.

The Faville Grove data (Figure 9) were variously arrived at and those for pheasants are considered the weakest, insofar as censuses of these birds were made in January of each year. Professor Leopold, from data available, worked out a rule of thumb method for calculating spring densities, 1937-41, on the basis of a 15% late winter loss plus a gain of 25% of the birds artificially stocked in midwinter. Fall densities were calculated by adding to the January censuses the shooting kills of the preceding falls. Releases of artificially propagated 8-week pheasants in August were disregarded. Several discrepancies between the data of Figure 9 and those given by Hawkins (44, pp. 45-49) for the area may be laid to errors missed in proofreading the earlier publication.

The known changes in the waning remnant of prairie chickens at Faville Grove, spring to fall, were slight in terms of numbers of individuals except in 1938 (tabulated data, right center of Figure 9). Moreover, the population was believed to be virtually

without competitive influence on the other resident Galliformes. For these reasons, the curve outlined by the rates of gain or loss of the wild Galliformes, collectively, may be considered more truly informative with the chicken data omitted.

From Figure 9, it is apparent that the curve for the bobwhite-partridge-pheasant combination shows clearer conformity to the principle of inverse ratios than do the curves for any one of these species plotted separately.

Turning again to Figure 6, we see, lower left, that rates of gain for the Prairie du Sac bobwhites and pheasants, collectively, line up better along the main curve, and seemingly along the other one as well, than do the rates for the bobwhite, alone. It would therefore seem that even very low densities of pheasants have their competitive significance to the bobwhite.

THE DENSITY FACTOR

Nearly a quarter-century ago, Pearl and Parker, from experimental data on both vertebrates and invertebrates, stated (64, p. 217): "In general there can be no doubt that this whole matter of influence of density of population, in all senses, upon biological phenomena, deserves a great deal more investigation than it has had. The indications are that it is the most significant element in the biological, as distinguished from the physical, environment of organisms."

To me, the conclusion seems inescapable that much may happen in the ecology of the bobwhite without visibly affecting population trends and that much may be superimposed upon basic natural rhythms, or, shall we say, upon biological undercurrents that are neither easily deflected nor changed in pace. The thresholds of security and the inverse ratios revealed by the Prairie du Sac data—and similarly though less completely and less clearly by data from other north-central areas—may be considered manifestations of such undercurrents.

The observed interchangeability in density equations of the bobwhites and certain of their exotic relatives, on a bird for bird basis, provides some clues as to how density may work as a limiting factor.

If we regard the Prairie du Sac pheasants, in a space-competitive sense, as extra bobwhites, we see accentuated the trends that were already well defined by the bobwhite data, alone.

We may not assume that pheasants, alone, would respond wholly in the same way. Indeed, we may be sure that they would not, for, in other parts of the region, they have displayed vastly more tolerance of crowding than have the bobwhites, sometimes massing locally by hundreds or thousands (29, pp. 96-98). In addition, the pheasants may not be as characteristically sensitive to "undercurrent" influences as the bobwhites. Neither the Ames nor the Faville Grove pheasants (left center, Figure 8, and lower left center, Figure 9) responded during the depressions of 1936 and 1937 in a way comparable to the apparent responses of the bobwhites.

It would seem that the rates of gain and loss of the pheasants, while doubtless not divorced from all

rules of order and automatic adjustment, were subject to considerable variation and that the conformation of rates of gain and loss of mixed populations of bobwhites and pheasants to the patterns shown by the Prairie du Sac data (lower right, Figure 5, and lower left, Figure 6) reflected population phenomena that were primarily those of the bobwhites. As the fortunes of the pheasants varied, adjustments in rates of gain and loss of the bobwhites tended to take place accordingly, within the framework set by the bobwhite's own limiting mechanisms.

It would be very easy to get out of our depth philosophically in attempting to consider the role of psychology in self-limiting mechanisms of the bobwhite. In another paper (29, pp. 98-100), I introduced the thought that much of the year-to-year constancy to be noted in threshold values, etc., might be explainable in terms of toleration "traditions" (no anthropomorphic connotations intended) on the part of dominant individuals. All of the evidence of which I know continues to support the "tradition" concept and no evidence impresses me as being contrary to it; however, the subject may here be dropped without further comment for the reason that the "traditions," if truly existent and significant, now would seem to affect merely the local distribution and behavior of the birds rather than the status of the species over large areas. Over the larger areas, populations have a way of following basic patterns, irrespective of many differences that are apparent on a more local scale.

We may ask how much the manifestations of basic patterns of loss and gain that we have before us only hint of McAtee's (55, p. 144) thesis that predation collectively tends to be in proportion to population, later restated by him (56, pp. 125-126) to the effect that the proportion rises and falls progressively with increase or decrease in numbers of the available food organisms?

Granted that the losses classed in this paper as nonemergency in type are not due exclusively to predation, how strictly are they in their totality a function of density?

Predation and other nonemergency losses suffered by bobwhite populations (or by mixed bobwhites and pheasants) in excess of thresholds at Prairie du Sac are characterized by elimination of birds above threshold levels and by relative safety of unhandicapped birds living below thresholds. Nicholson's (61, p. 171) comparison of territory-holding birds with water in an overflowing reservoir is descriptive, with overflow birds like overflow water comprising the part of the whole that is lost.

The threshold type of predation has been considered a modification of the proportional predation type (21). As populations exceed thresholds, they are preyed upon more and more in proportion to numbers, but the populations wintering securely below threshold levels (sometimes with absolutely no loss for months at a time) certainly are not preyed upon proportionally.

Theoretically, one might expect, because of dif-

ferences in ability of mature birds in regular residence and the not so well established young to take care of themselves, that summer loss rates should be more in proportion to numbers than nonemergency winter loss rates.

Of course, we would be in a better position to inquire into the role of density in determining summer loss rates of bobwhites if we knew more about bobwhite and pheasant densities—of young birds and old—during summer and early fall of each year. In view of the scantiness of existing data, the best we can hope to do is to keep within the limits set by the actual figures for spring and late fall (or early winter) densities and to attempt some computation of densities and loss rates for the intervening periods on the most reliable prorata bases that we can find—without, however, losing sight of the essential unreliability of prorata computations treating with population trends that are marked by much automatic adjustment (31).

The summer of 1931 not only represented, in terms of bobwhite densities, weather, etc., about an "average" summer at Prairie du Sac, but also was one of most concerted field studies of bobwhite reproduction carried on during the entire program of work in southern Wisconsin and central Iowa.

Data gathered mainly during this summer and mainly from the neighborhood of Prairie du Sac gave the following statistics: bobwhite hens successful in bringing off broods, about 80% (not to be confused with percentage of nests succeeding); young hatched, 13.6 per successful hen; young alive by midsummer, about 70% of those hatched; adults alive by midsummer, about 90% of the spring population. A sex tally of mature bobwhites gave 42.3% hens. Using these values, we get a midsummer density 4.1 times as great as the spring density.

Let us try the latter as a constant in computing midsummer bobwhite densities for different years at Prairie du Sac. We need not really assume, knowing the extreme unlikelihood thereof, that the breeding population for each summer consisted of the identical birds present in spring or even of substantially the same number. Nor need we really assume any year-to-year constancy in adult sex ratios, percentages of hens successful in hatching young, sizes of broods hatched out, mortality rates of adults or young at given seasons, or of other things that we know are actually quite variable. Knowing the great amount of counterbalancing that occurs, we can expect "good" nesting seasons accompanied by little loss of clutches from enemies, weather, accidents, and miscellaneous disturbances to mean early termination of nesting activities and a high "reproductive efficiency." Conversely, during a season of unusual disturbances, we can expect the total number of eggs laid to become greater because of stimulation of increased nesting by abandonment or destruction of clutches, thus resulting in a poorer "reproductive efficiency," though not necessarily in much if any diminution in total numbers of young ultimately hatched during a season (31). And because of the

stringing out of the nesting season of southern Wisconsin bobwhites from May to September, we also know that the earlier of a season's young suffer mortality months before the later ones hatch.

Let us nevertheless see what we would get if we ignored these variables and went ahead with our computations.

Computation of approximate loss rates of Prairie du Sac, Wis., bobwhites, midsummer to early winter. (See comments in text.)

Year	Actual spring density	Computed midsummer density*	Actual early winter density	Percent of loss, midsummer to early winter
1930	112	467	257	45%
1931	236	949	400	59%
1932	290	1189	406	66%
1933	339	1390	433	69%
1934	288	1151	411	65%
1935	76	804	116	86%
1936	70	287	145	79%
1937	45	125	163	72%
1938	39	160	138	74%
1939	97	376	310	50%
1940	133	543	273	50%
1941	162	582	264	55%
1942	122	520	353	29%
1943	70	287	177	38%

* Spring density multiplied by 41, according to rough index derived in text.

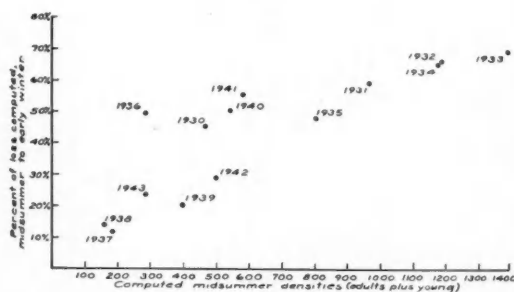


FIG. 10. Computed loss rates of bobwhites in relation to density, Prairie du Sac, Wis., midsummer to early winter, 1930-43. Values obtained through computations should be considered with reservations, as indicated in text.

In Figure 10 are plotted, with reference to known and computed densities at Prairie du Sac, the computed loss rates, midsummer to early winter. The length of the period to which the loss rates apply is intended to be about the same as that used in plotting the winter losses of Figure 5, or approximately four and one half months.

Even while keeping in mind all appropriate reservations, we may be confident that shortcomings of the prorata computations were not the main cause of loss rates in Figure 10 failing to occur in anything resembling straight proportions to density. Be it conceded that the rate for 1936 might reflect something close to proportional losses, the rates for at least 1930 and 1940-41 are patently lower in proportion to numbers involved; those for at least the 1931-35 span, still lower. All of the computed loss rates between 45% and 69% are for computed midsummer densities ranging from 287 to 1,390 birds.

In looking over the rates of nonemergency winter losses and of summer gains plotted in Figures 5 and 6, we may see that the two major curves defined by the data points in each case, density-linked though they are, assuredly are the product of more than density.

There are at least two phases of density response, one shifting into the other and out again, to be traced through Figures 5 and 6. The one that we may call the "normal" or "phase I," defined by the winters of 1929-36 and 1937-38 and the summers of 1931-35, 1937, 1939, and 1942, if not by the winters of 1939-40 and 1942-43, clearly is not due to the same function of density as is the phase of depressed winter thresholds and summer gains that we may call "phase II"—the winters of 1938-39, 1940-42, 1943-44, and the summers of 1930, 1938, 1940-41, and 1943. The summer of 1936 and the following winter, which, at Prairie du Sac, show the lowest rates of summer gain and the highest rates of nonemergency winter loss in relation to density, may conceivably represent a third phase.

SYNCHRONY AND PERIODICITY SHOWN BY DEPRESSION PHASES OF HIGHER VERTEBRATES IN NORTH-CENTRAL UNITED STATES

The literature on periodic cycles is tremendous, includes much pioneering and obsolete work and much that, because of deficiencies in my own knowledge, I find unappraisable. It relates chiefly to species other than the bobwhite—indeed, the bobwhite is often regarded as noncyclic, doubtfully cyclic, or only slightly cyclic on the basis of the evidence shown by gross fluctuations.

Gross fluctuations are probably as important a cause of dissension on this subject as any single thing. Kendenigh's (47, p. 4) bobwhite curve for Ohio, 1908-31, and Leopold's (50, p. 142) curve for the frankly cyclic ruffed grouse in Wisconsin for the same period have broadly synchronous declines and ascendancies. On the other hand, the bobwhite over its range as a whole is referred to as a species with a flat population curve (51, p. 70). Further, the gross fluctuations of both grouse and bobwhite may vary, for example, according to geography (51, pp. 59-71).

In my opinion, it is all but hopeless to try to gain an accurate idea of possible periodicity solely or even mainly by consideration of gross fluctuations of a species as susceptible to emergency depression as the bobwhite in north-central United States and it, therefore, behooves us to seek other common denominators.

No attempt will be made to undertake a general treatment of animal cycles in this paper. And although evidence from other species will be freely used, the primary objective of this section will still be to aid in the exploration of population phenomena of the bobwhite.

In laying the groundwork for this and other writings, I have searched through literature and unpublished notes, alike, for numerical data on rates of increase of vertebrates on definite areas of land over periods covering two or more breeding seasons.

Small to medium-sized mammals and birds, especially the more prolific, seem to show a quite pronounced tendency to increase in numbers, spring to

Year	April density	June density	October density	Percent gain (or loss) April to October	Percent loss June to October	Percent loss Oct. to following April
1930	244	1195	462	88%	61%	17%
1931	384	1644	666	73%	59%	17%
1932	555	2165	910	64%	58%	30%
1933	640	2213	979	53%	56%	35%
1934	640	2042	666	4%	67%	66%
1935	210	744	196	7% loss	74%	50%
1936	98	349	76	22% loss	78%	—

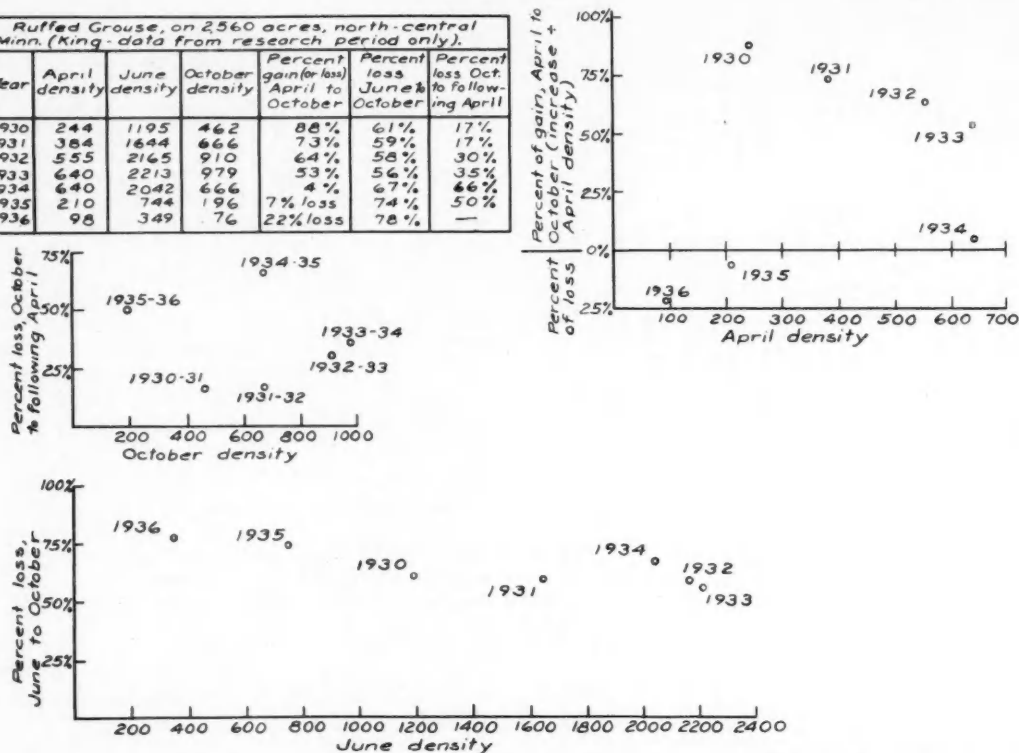


FIG. 11. Rates of gain or loss of ruffed grouse in relation to density, north-central Minnesota, different seasons, 1930-36. Data presented are for the period of actual study only, as published by R. T. King.

fall, in inverse ratio to their spring densities. They also show "off points" suggesting affinities with the phases noted for the Prairie du Sac bobwhites and possibly other phase effects.

The classic examples of periodically cyclic species, the ruffed grouse and snowshoe hare (*Lepus americanus*), are hardy northern wilderness forms ordinarily having access to an abundance of staple food in the most habitable parts of their geographic ranges. They are not completely unaffected by emergency factors, such as extremes of weather, but their susceptibility certainly is much less than that of the granivorous bobwhite in the north-central states. If gross fluctuations of any species truly reflect cyclic behavior, they should be those of the ruffed grouse and snowshoe hare in characteristic environment.

Figure 11 was prepared from King's (49, p. 529) data on ruffed grouse of an area in north-central Minnesota during a period of cyclic ascendancy and decline. It may be seen that during the recorded ascendancy—spring, 1930, through winter, 1933-34—the summer gains (upper right) showed broadly inverse ratios and the winter losses (left center) showed threshold phenomena. Both curves resembled those of phase I for the Prairie du Sac bobwhites. The summer loss rates for 1930-31 were greater than one might have expected for the moderate densities in-

involved, so we may consider the possibility that the grouse were still in a somewhat depressed phase during the first two years of the census records. This thought is supported by the facts that the 1930-31 rates of gain look a little lower in relation to April densities than do those for 1931-33, and that the rates of winter loss, 1930-32, look a little high—at least, they do not reflect the degree of security that non-emergency losses of northern bobwhites typically do at subthreshold levels. The collapse of the population seems to have begun in the summer of 1934 and swiftly gained momentum. The lowest densities and the severest rates of loss recorded were reached in 1936, at the depth of the cycle or very close to it.

Fisher's published data on ruffed grouse in Michigan are presented collectively in Figure 12 for all long-studied areas from which census figures were taken by means of his preferred Method II (37, pp. 11-12). The data points in the upper left show progressively depressed rates of summer gain for the spring densities involved as the cyclic decline approached its culmination, which seemed to have been in 1936.

The data from the New York studies on the Connecticut Hill area reported by Edminster (12, p. 826—corrections made upon that author's advice) are likewise presented in Figure 12. Rates of summer gain

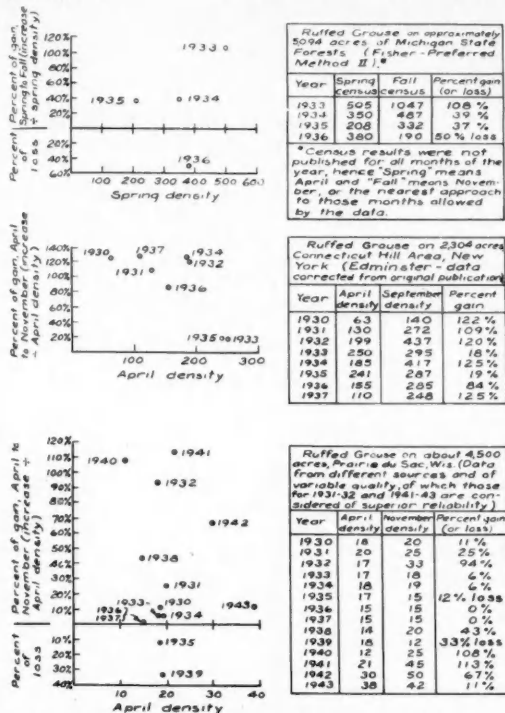


FIG. 12. Rates of gain (or loss) for ruffed grouse in relation to density on areas in Michigan, New York, and Wisconsin. See text for additional comments as to data.

(see left center) for 1930-31 seem, as do King's data for those years, to reflect a depressed phase. The rates for 1932-35 define what may be only a steep-sloping curve determined mainly by density; unfavorable weather conditions to which Edminster (12, p. 827) ascribes the low rate of gain for 1935 should not be disregarded but neither should the notable similarity of the low gains of 1933 and 1935 from the very high April densities. The points for 1936-37 suggest another change of phase, this one probably reflecting part of another cyclic decline.

Even the data from Prairie du Sac's low-density grouse population, inferior that many of them are, reveal much the same phenomena (lower left, Figure 12). From 1930 through 1932, phase changes seemed to grow increasingly favorable; then 1933-37 may be said to reflect a depression phase; apart from the loss of 1939, the gains for 1938-40 were increasingly strong for the densities; and, finally, the 1941-43 gains, presumably occurring at the most favorable time of the cycle, show typically inverse ratios for high (for the area) April densities.

Considering now the Connecticut Hill data on winter loss rates of ruffed grouse (Figure 13), we can see a tendency for the loss rates for comparable fall levels (272 to 295 birds) to rise as the population evidently heads toward a cyclic decline. Despite some variables in these data that I am in no position

to evaluate, I would say that phase phenomena at Connecticut Hill show much the same sort of shifting and linkages as they do for the Minnesota grouse.

Winter losses for the ruffed grouse of the Michigan State Forests and for Prairie du Sac are not plotted, but, from the data (upper and lower right, Figure 12 and preceding text) some trends are easily perceptible. Fisher's 1933 spring census of 505 birds denotes a favorable phase and one followed by a high spring to fall rate of gain; the survivals for the next three winters suggest depressed phases as do the data for the following breeding seasons. At Prairie du Sac the wintering grouse populations responded pretty well to thresholds of around 18 to 20 (possibly lower in some years when lower densities wintered with little or no recorded loss) until the last three-year period; whatever may be said of the high winter survivals and the high rates of summer gain in relation to density, 1940-44, together they seem to reflect a major and a most favorable phase.

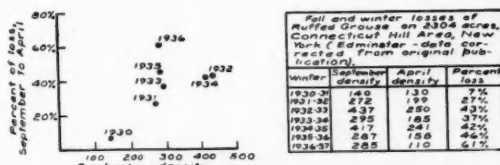


FIG. 13. Rates of fall and winter loss of ruffed grouse in relation to density, Connecticut Hill area, New York, 1930-37.

Clarke's conclusion from his studies of the ruffed grouse in Ontario that "In a year of dying off, the number of young surviving is only half of that of a normal year" (8, p. 107) is weakened by his apparent neglect of possible density effects. However, his statement that "even though the first year of dying off in an area has reduced numbers to a point where the birds may be regarded as scarce, the succeeding year may show a similar reduction in summer flocks" (8, p. 77) has its parallel in the figures for the low of the cycle obtained from north-central United States. He reported much variation as to time of onset of the decline of the ruffed grouse in different parts of Ontario and that on the whole diminution in the Province occurred in 1933-34. His graphs of abundance for Ontario (8, pp. 21, 23) have no dates later than 1934, but it is rather obvious that the grouse over most of Ontario had not reached their minima by that time.

The decline of the other classically cyclic North American species, the snowshoe hare, was pronounced on Green and Evan's Lake Alexander area in northern Minnesota from 1935 to 1938 (38). These authors later wrote (39, p. 356) that "of the young born in the summer of 1937 [when the species was approaching minimum numbers] only eight percent lived to February, the lowest rate of survival recorded in the seven years of our investigations."

By 1935, the hares of the Hudson's Bay watershed were well along in a cyclic decline (54, p. 17).

Turning back to Figures 5-9, we may perceive that 1936 had unusual significance in population phenomena either of bobwhites alone or of bobwhites in combination with other wild Galliformes at Prairie du Sae, Hunt City, Ames, and Faville Grove. Figures 14-15, dealing with perdicine birds of Des Moines, Iowa (29, p. 86), southern Iowa (65, p. 720), Pine Bluff and Honey Creek Bottomlands of southern Wisconsin (18, pp. 17-21), Blissfield, Mich. (68, p. 77), and Stillwater, Okla. (4, pp. 113-115) show more evidence of a synchronously depressed phase in 1936 than in any other year.

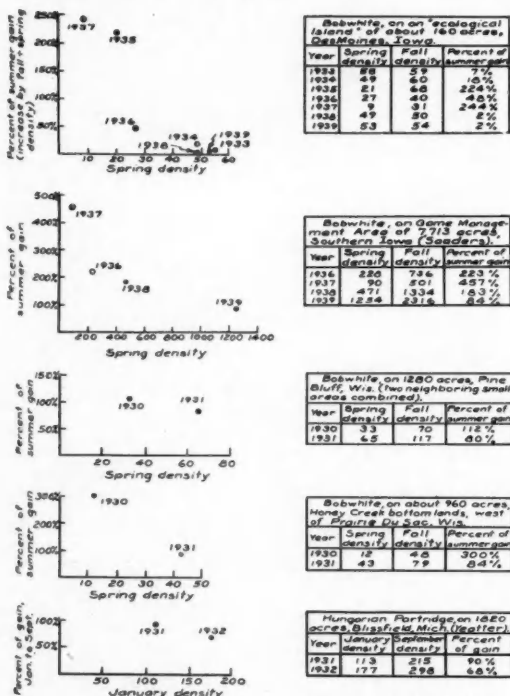


FIG. 14. Rates of summer gain of perdicine birds in relation to density on areas in Iowa, Wisconsin, and Michigan.

At Hunt City and Ames (Figures 7-8), 1937 also was a year of pronounced depression of bobwhites or of combined wild Galliformes.

It is hard to judge what other north-central Galliformes showed in the way of depressions at the time of the cyclic minima for ruffed grouse and snowshoe hares. The percent of gain for the Faville Grove prairie chickens (see data, right center of Figure 9) was higher in 1936 than in any other year listed except one, but the low and waning status of these birds makes such a gain of dubious significance. At Hunt City (left center, Figure 7), rates of summer gain for the chickens were low for the spring densities in 1936 and 1937. There were probably some variables here due to the high mobility of the species and the small size of the area, which Yeatter (69,

p. 394) is careful to remind us "represents the smallest unit indicated by Davison's study as representative."

The study by Davison referred to was one of a different species of prairie chicken (*Tympanuchus pallidicinctus*) near Arnett, Okla. April-May censuses of cocks from 1932 to 1939 reveals lowest numbers between 1936 and 1938 (no data for 1937) (10, p. 59); and, for the four-year period, 1932-35, fewer young were found per covey during the years of declining density, 1934-35 (10, p. 58) (Figure 16).

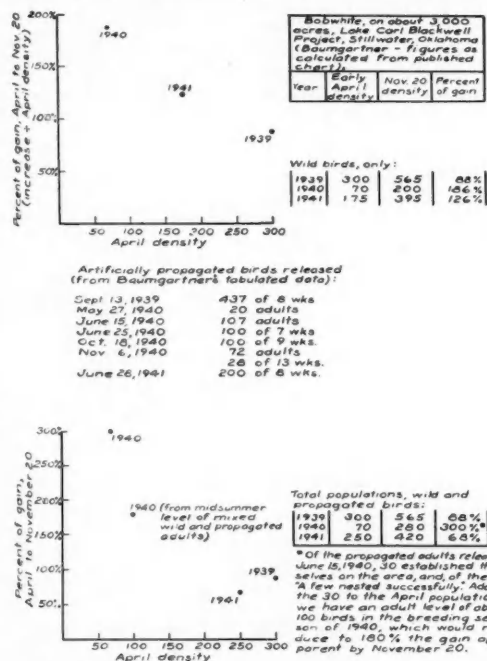


FIG. 15. Rates of summer gain of bobwhites in relation to density on an area near Stillwater, Okla.

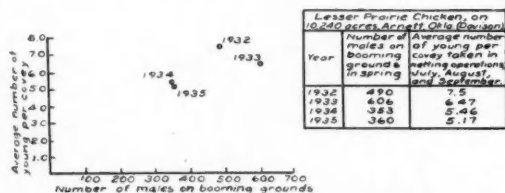


FIG. 16. Variations in average numbers of young in coveys of lesser prairie chickens in relation to densities of adult males on an area near Arnett, Okla., late summer and early fall, 1932-35.

The pheasant data from Prairie du Sae, Ames, and Faville Grove (Figures 6, 8, and 9) are insufficiently precise to justify many conclusions as to how much the rates of gain of the pheasants may have been depressed during low years of the cycle for grouse and hares, but, in general, the evidence indicates that the pheasants were not entirely exempt from depres-

sive influence at this time. In northwestern Iowa, Bennett and Hendrickson reported a poor recovery for pheasants during the breeding season of 1936 and an actual loss during that of 1937; despite the role ascribed to weather (5, p. 723), there could be much more behind the depressed rates of gain than weather or the factors commonly looked for.

Recently Bach's (3, p. 8) figures on fluctuations of pheasants in North Dakota suggest depressed rates of summer gain for low May densities in 1938 (the earliest year for which data are given); gains in inverse ratio to somewhat higher densities in what may be interpreted as a more favorable phase, 1939-40; and, finally, gains in inverse ratio to still higher densities at what seems to be a very favorable phase, 1941-43. The latter data, so far as they go, depict essentially the type of gains to be expected for ruffed grouse at different levels and different phases.

Figure 17 relates to a number of species of western United States. The two years of data gathered by Yokum (70, p. 195) for Hungarian partridges and pheasants at Pullman, Wash., show, in combination, rather typical inverse ratios (right center and lower right). The 1942 depressed gain for a low density of scaled quail (*Callipepla squamata*) in New Mexico (lower left) suggests cyclic influence having no synchrony with any cyclic phase that I recognize in the north-central states; Johnson, in presenting the data, wrote that the 1942 decline was "accompanied by an extraordinary reduction of cottontail rabbits" (46, p. 25).

Emlen's data on California quail (*Lophortyx californica*), as calculated from his chart (15, p. 96) and reproduced in the left center of Figure 17, shows no depression of rates of gain in 1936, but about the sort of depression in 1937 and 1938 that many north-central Galliformes experienced in 1936 and to some extent in 1937. Horn (45, p. 745) refers to a poor hatch coinciding with a materially decreased adult population of California quail on another area in 1937.

The two years of data available from California on Erickson's wren tits (*Chamaea fasciata*) (16, p. 311) and on Evans and Holdenried's Beechey ground squirrels (*Citellus beecheyi*) (36, p. 247) suggest only typical inverse ratios (upper left and right, Figure 17).

Burt's chipmunks (6, p. 46) and Haugen's cottontails (43, pp. 108-114) in Michigan showed inverse ratios, the former species in 1936 and 1937 as well as in 1935 (upper left, Figure 18). It may be recalled that 1936 was a poor year for cottontails at Prairie du Sac and elsewhere in southern Wisconsin (see discussion of "buffers" in this paper).

Hamilton's meadow mice in New York (41, p. 782) certainly were depressed in 1936, whatever the data for the other years may signify with respect to phases (lower left center, Figure 18).

In lower Figure 18, data are given for the long-tailed field mouse (*Apodemus sylvaticus*) in England for three years antedating the Prairie du Sac study (14, p. 676). The one point that departs from in-

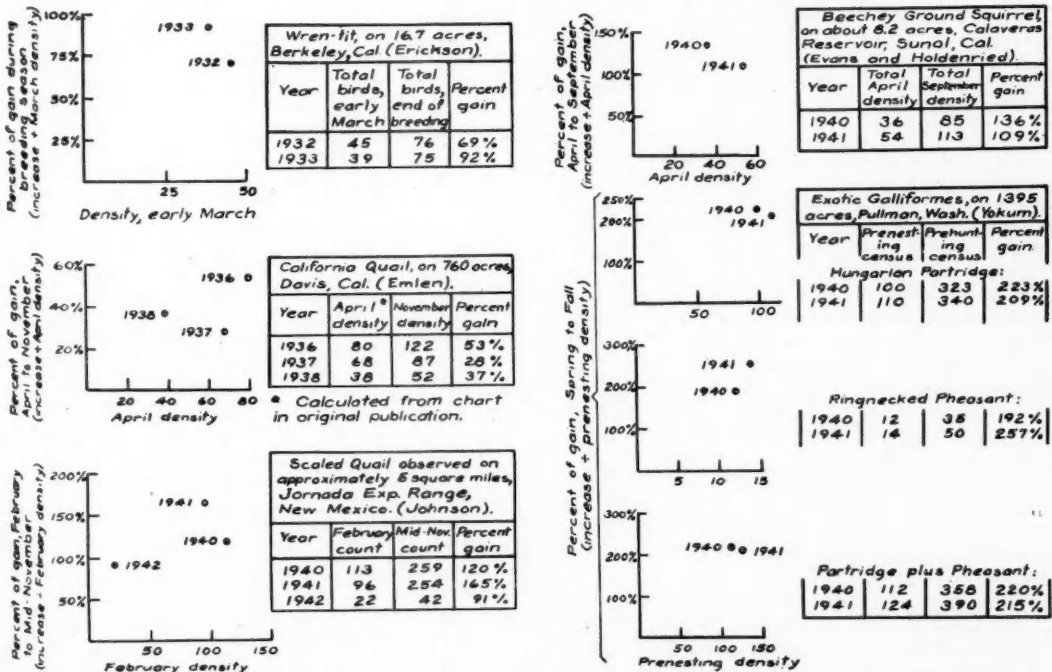


FIG. 17. Rates of summer gain of miscellaneous higher vertebrates in relation to density on areas in western United States.

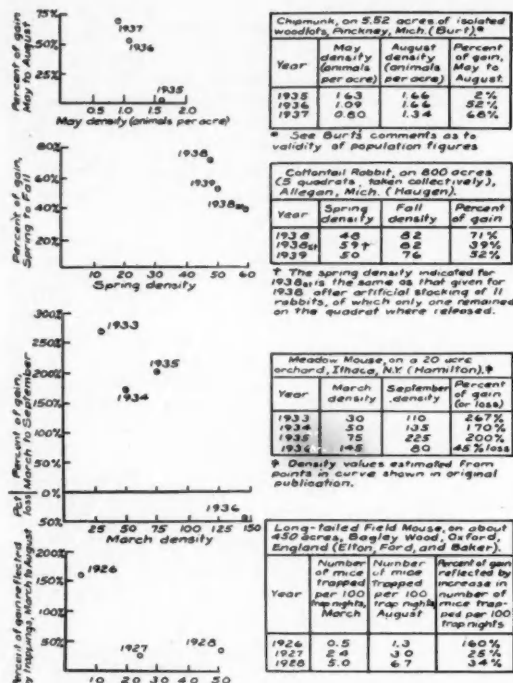


FIG. 18. Rates of summer gain (or loss) of miscellaneous mammals in relation to density on areas in Michigan, New York, and England.

verse ratios—that for 1927—coincidentally or not, synchronizes with the low of the cyclic decline of north-central states and snowshoe hares preceding that of 1936-37.

The only north-central data on rates of gain obtained during the low years of the preceding cyclic decline are Kendeigh and Baldwin's (48, p. 100) for the house wren (*Troglodytes domesticus*) at Gate Mills, Ohio. The numbers of young raised per adult as plotted in Figure 19, upper left, do not conform too clearly to inverse ratios, but the years of lowest adult densities and two of the lowest rates of gain were 1926 and 1927, the low of the cycle for North American grouse and rabbits, generally (51, p. 65).

Chapman's (7, pp. 61, 65 and 71) data on numbers of young tree swallows (*Iridoprocne bicolor*) raised per nesting box or pair at Princeton, Mass., show what I would interpret as inverse ratios during a favorable phase, 1934-35, and inverse ratios during an unfavorable phase, 1936-37 (Figure 19, left center). The poor success of the lowered population of 1938 was linked with a weather emergency (7, p. 65).

McClure's intensive study of the mourning dove (*Zenaidura macroura*) on comparable areas at Lewis, Iowa, 1938-39, did not coincide with any years of known cyclic depression of Galliformes in this region. Average numbers of young raised per pair conformed to inverse ratios, irrespective of whether the original (57, pp. 65, 67) or the revised (58, p. 384) estimates

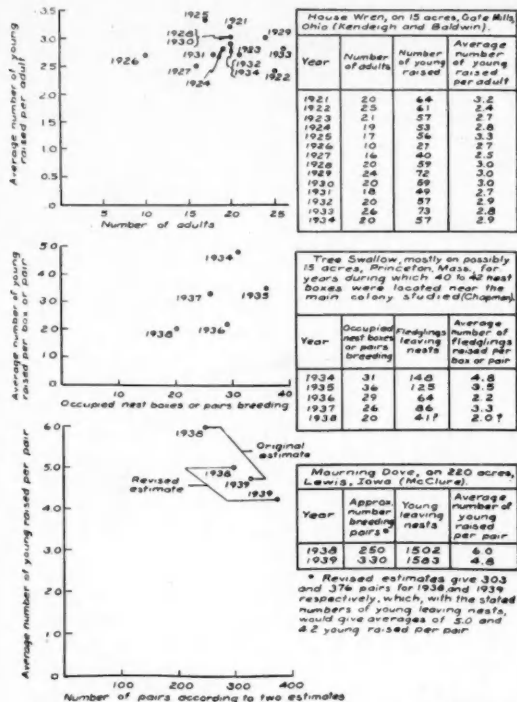


FIG. 19. Average numbers of young raised by miscellaneous birds in relation to density on areas in Ohio, Massachusetts, and Iowa.

of breeding densities were used (lower left, Figure 19). The 1940 investigations were not conducted on areas comparable to those of 1938-39, but this author estimated a slight decline from the over-all breeding level of 1939, with a considerably lowered rate of productivity (58, pp. 357-358, 362-367). Any connection with the latter and the phase II performances of bobwhites at Prairie du Sac in 1940 is totally unproved, but such a possibility may be worth thinking about, especially in view of the seeming operation of phase II at Ames in that year (Figure 8).

Mrs. Nice's remarkably detailed investigation of the song sparrow (*Melospiza melodia*) at Columbus, Ohio (60), lacks data on postnesting populations, but the percentages of song sparrow eggs producing either young song sparrows or, indirectly, young of their nest "parasite," the cowbird (*Molothrus ater*), may be at least partly indicative of reproductive success. The figures on April densities in Figure 20 were derived from the data on breeding males given on her page 200 and sex ratios on her page 173; figures on productivity of the eggs, from her pages 141, 150, and 159.

Detection of possible phase effects in the points plotted (center, Figure 20) is made most uncertain because of the drastic changes in the habitat resulting from human debrushing and other activities in the summer of 1932 (60, p. 10). Disturbance of cover was less in 1935 than it had been in 1933 and

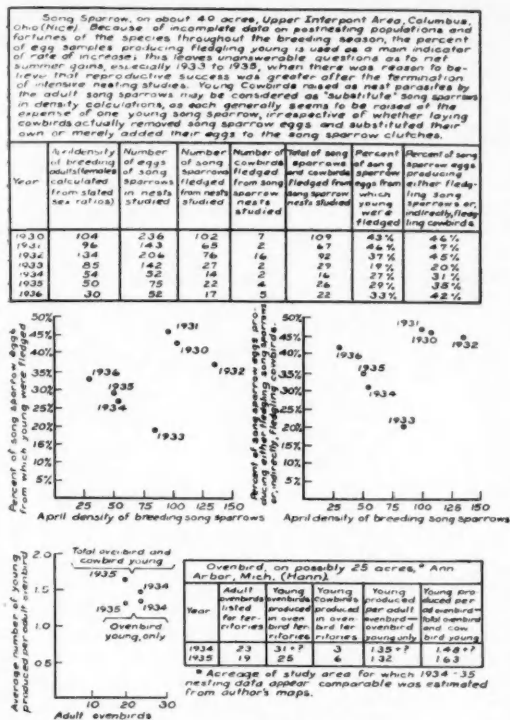


FIG. 20. Success of reproduction of passerine birds in relation to density on areas in Ohio and Michigan, considered both in terms of the nesting species and their "parasite," the cowbird.

1934, however (60, p. 201), and, if this meant a real trend toward environmental restoration, the relatively low percentage of egg success for the low-density season of 1936 could reflect more of a depression phase than the alignment of the 1933-36 points would otherwise suggest.

From examination of Hann's records of ovenbird (*Seiurus aurocapillus*) and cowbird production on the approximately 25 acres of land near Ann Arbor, Mich., that he had under observation both in 1934 and 1935 (42, pp. 219-220, 224-225), we may see that the average number of young of the ovenbird and its "parasite," together, were in typical inverse ratio to the numbers of adult ovenbirds, although ovenbirds, considered alone, did not show this (lower left, Figure 20).

Figure 21 presents the most reliable data in my possession on summer gains of muskrat (*Ondatra zibethicus*) populations on three areas in Iowa kept under regular observation over substantial periods of time. (Other Iowa areas have also yielded long-term, year-to-year data on population phenomena of the species but the data from these have been so dominated by emergencies—during droughts, in particular (28, 32)—as to show little or nothing of the course of basic curves.)

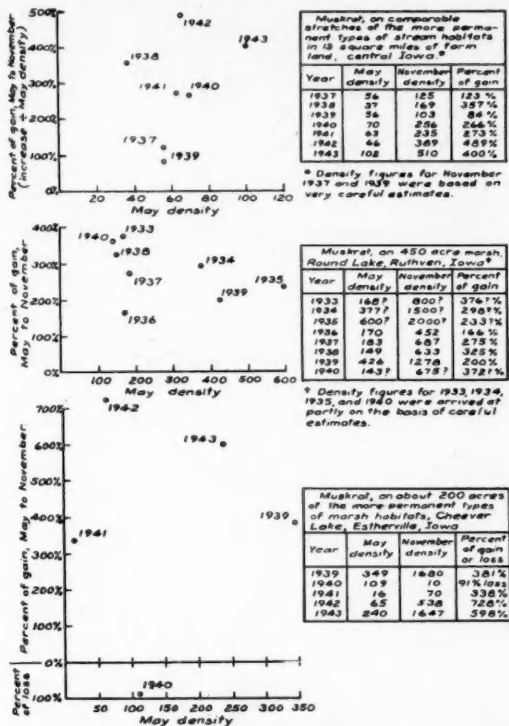


FIG. 21. Rates of summer gain (or loss) of muskrats in relation to density on Iowa areas. Consult text for information on emergency losses resulting from droughts and floods.

The central Iowa stream data (upper left, Figure 21) exemplify rates of gain under emergency and nonemergency conditions. The seasons of 1937 and 1939 were ones of prolonged, extreme droughts in late summer and fall, and the muskrats suffered conspicuously. Only on one central Iowa stream observed—a drainage ditch near Story City—did water conditions remain favorable in 1937 and here the rate of gain of the animals was high (25, pp. 418-419). Severe floods in 1940 and 1941 after the breeding season resulted in considerable losses of the immature, but it is not demonstrated that the depressed rates of gain in relation to density were due wholly to this cause.

The central Iowa gains for 1938, 1942, and 1943 were probably typical for seasons essentially free from emergency depression; actually, severe mortality of helpless young from floods occurred in May and June, 1942, but those losses were compensated by increased productivity in the latter part of the breeding season. The gains for 1942 and 1943 seem to be typically in inverse ratio to the May or breeding densities; that for 1938 is believed to reflect the inefficient mating of low densities.

(In contrast with the bobwhite, which may be obviously successful in its mating at exceedingly low

densities, the muskrat in Iowa has not shown good rates of increase at densities averaging less than the equivalent of about one pair per linear mile of small stream habitats or about one pair per 15 acres of marsh lands. This is regarded as one of the outstanding manifestations of underpopulation, of the types studied notably by Allee and co-workers (1, 2.)

At Round Lake, the population suffered from drought in 1936, but most of the animals lived in parts of the marsh having deep enough water to afford them protection (28, p. 176), and the poorness of the recovery certainly may be thought to reflect the influence of more than drought (Figure 21, left center). Neither may the gain for 1937 be quite as high as could normally be expected for the May density and favorable breeding and rearing conditions. A more severe and prolonged drought occurred in late summer and fall of 1939 than in 1936 and the rate of gain was depressed to an imperfectly ascertained extent by shallow zone losses (32, p. 855). Other than during emergency seasons or probable depression phases, the rates of gain tended to show typical inverse ratios.

The Cheever Lake gains for 1939, 1942, and 1943 on about 200 acres of habitat showing relatively little change from year to year look rather typical despite much dry weather in 1939 (lower left, Figure 21). The depressed rate for 1941 is ascribed mainly to underpopulation phenomena; that for 1940 to a lethal drought (32, pp. 858-865). I do not know whether other factors were important in determining the population trends for 1940 and 1941.

We may naturally be hesitant about drawing many conclusions from the available data on rates of increase from given density levels of higher vertebrates, but it does appear that few north-central species thrived in 1936. The 1936 drought cannot be entirely dismissed from consideration as a depressive agency; nevertheless, the breeding season in this region had features not explainable in conventional terms of weather. Furthermore, the 1937 gains were abnormally low for some species in some north-central localities where weather conditions varied a great deal.

We then have some justification for concluding that there may be a real linkage between the phase III (summer of 1936, winter of 1936-37) of the Prairie du Sac bobwhites, the low of the cycle for the region's ruffed grouse and snowshoe hares, and the clearly depressed rates of gain of various other mammals and birds in 1936 and to a considerable extent in 1937.

If there is any connection between the phase II of the Prairie du Sac birds (summers of 1930, 1938, 1940-41, and 1943, and winters of 1938-39, 1940-42, and 1943-44) and similar depression phenomena to be noted elsewhere, I, at any rate, do not feel sure of it. Just enough scattered evidence exists, especially for 1940 and 1941, to keep the question open.

My reconstruction of the cyclic picture for the region (and possibly for other parts of North America, as well) takes the following outlines:

(a) For the classically cyclic ruffed grouse (and presumably the snowshoe hare) one phase graded off into another, rates of summer gain falling and rates of winter loss rising in relation to density as the depth of the cycle was approached. Then, after a period of extreme depression, rates of summer gain tended to rise and rates of winter loss to fall as the ascendancies got under way. Each distinguishable phase seemed to last from a few months to two or three years, with the extreme depressions showing the most synchrony between local areas. Very likely, the extreme depressions also showed the most periodicity—although gross fluctuation remains, up to recent years, the main criterion by which periodicity may be judged.

(b) For the bobwhite, about the only evidence of periodicity was furnished by what may be called the phase III, representing the extreme depression synchronous with the low of the cycle for the region's ruffed grouse and snowshoe hares. This phase seemed to cover one or two years. The less pronounced but more frequent phase II depressions of summer gains and winter thresholds might conceivably be compared with some of the intermediate phases suggested by the grouse data except that they occurred with much greater irregularity and without the ascending and descending sequences with respect to the period of extreme depression.

(c) For wild higher vertebrates of small to moderate sizes, generally, the years of extreme depression look pretty well synchronized, species with species and area with area. They have at least a semblance of an approximately 10-year periodicity. Other apparent phases showed variations with species, some indicating progressive changes and others a possible agreement with the in and out shifts of the Prairie du Sac bobwhites between phases I and II. And still others, let us not forget, experienced depression phenomena or unusually high rates of gain that did not seem to agree with any phase detected in the records for other species or for other areas.

THEORY OF DEPRESSION PHASES

The reader should not expect this section to answer more than a few of the questions that the preceding discussions may have brought to mind. Little enough concerning depression phases is really clear. Not only are we virtually without information as to causes, but serious deficiencies also exist in our knowledge of elementary properties.

What, then, can we legitimately conclude at this time, with the least likelihood of contradiction by future researches? Probably certain of the mathematical aspects of the phase phenomena are as revealing as anything currently at hand.

In the latter connection, I wish to express appreciation for curve-fitting and related cooperation by Professor F. A. Brandner, Department of Mathematics, Iowa State College. To him should be credited all of the mathematical treatment of the north-central data here following.

Sigmoid curves of the types used by many students

of populations, notably Pearl (see 62, pp. 558-637; 63, pp. 75-82), were fitted to the phase I and II data for rates of nonemergency losses and summer gains at Prairie du Sac. It was found, however, on account of phenomena associated with thresholds, that a lower asymptote different from zero was required, at least within the numerical range covered by the data.

The general form of equation for the curves is:

$$y - y_0 = \frac{K}{1 + Ae^{bN}}$$

where y = percent of loss or gain, N = density, e = the base of natural logarithms, and K , A , and b are parameters estimated in the process of fitting.

The curve in lower right, Figure 5, defined by the clearly phase I nonemergency loss rates (which are shown as beginning in early winter of the years 1929-35 and 1937) of bobwhites and pheasants, collectively, does not seem to conform to a single equation. At subthreshold levels (below, let us say, 300 to 330 birds), the rates of loss are very slightly if at all accelerated with increasing density, and no formula was found that gave more than a poor fit for the curve as a whole. But for the five data points for densities exceeding threshold levels and hypothetical points calculated for 350- and 450-bird levels on the basis of probable threshold behavior, the curve conforms fairly well to the sigmoid:

$$y - 5 = \frac{31}{1 + e^{19.67 - .0486N}}$$

where y = percent of loss during approximately $4\frac{1}{2}$ winter months and N = density at the beginning of the winter. The error of estimate is 22.7% of the standard deviation.

Phase II loss rates, beginning early in winter, 1938, 1940-41, and 1943, conform (so far as they go) to another sigmoid:

$$y = \frac{54}{1 + 19.11e^{-0.0179N}}$$

with an error of estimate of 10.9% of the standard deviation.

In the absence of definite data on rates of non-emergency winter loss rates for phase II at lower densities, we may get some idea of the possible lower asymptote by extrapolation—in any event, the curve approaches the lower asymptote at low densities.

Two points other than the one for phase III, 1936, are left out of the above curves: those for loss rates beginning early in the winters, 1939 and 1942. We have some grounds for believing that the latter represent transition winters (both were followed by phase II summer gains) between phases I and II rather than random departures from phase I.

The summer loss rates of bobwhites, as computed for Figure 10, may here be considered much as were the winter rates. For phase I (1931-35, 1937, 1939, and 1942), a reasonably close-fitting curve seems to be:

$$y = \frac{73}{1 + 8.94e^{-0.0034N}}$$

where y = percent of loss during approximately $4\frac{1}{2}$ months of late summer and early fall and N = computed midsummer density. The error of estimate is 9.7% of the standard deviation.

For phase II (1930, 1938, 1940-41, and 1943), the formula:

$$y = \frac{90}{1 + 11.8e^{-0.005N}}$$

seems applicable, with an error of estimate of 8.0% of the standard deviation.

The phase I curve in lower left, Figure 6, for rates of gain of bobwhites and pheasants, April to November, 1931-35, 1937, 1939, and 1942, is described by the formula:

$$y - 20 = \frac{251}{1 + 0.049e^{0.0187N}}$$

the error of estimate being 5.0% of the standard deviation. In this equation, y = percent of gain during summer and early fall from the April density, which latter is represented by N .

The rates of gain for phase II (1930, 1938, 1940-41, and 1943) responded less conveniently to curve-fitting, the formula obtained being:

$$y - 15 = \frac{265}{1 + 0.15e^{0.0206N}}$$

with an error of estimate of 14.0% of the standard deviation.

Figure 22 represents an attempt to learn something more regarding the lower asymptote of the curve for phase I. To the Prairie du Sac data were added data from Ames, where combined populations of bobwhites and pheasants showed rates of gain comparable to those of the Prairie du Sac birds at some comparable densities yet reached higher spring densities on two occasions.

The data points for Ames, 1933-35 and 1938, are considered in phase I and together with the phase I points for Prairie du Sac, conform to the curve:

$$y - 20 = \frac{241}{1 + 0.052e^{0.83N}}$$

with an error of estimate of 15.4% of the standard deviation. Spring densities (N) were given in birds per 100 acres.

Of the other points for Ames, that for 1940 is thought to represent phase II; those for 1936 and 1937, phase III, as does that of 1936 for Prairie du Sac. The significance of the high point (in relation to density) of 1939 is obscure. Could this possibly be a manifestation of an infrequently occurring fourth phase, an exceptionally favorable one? Or are we heading for error in attempting overmuch to place rates of gain into phase groupings?

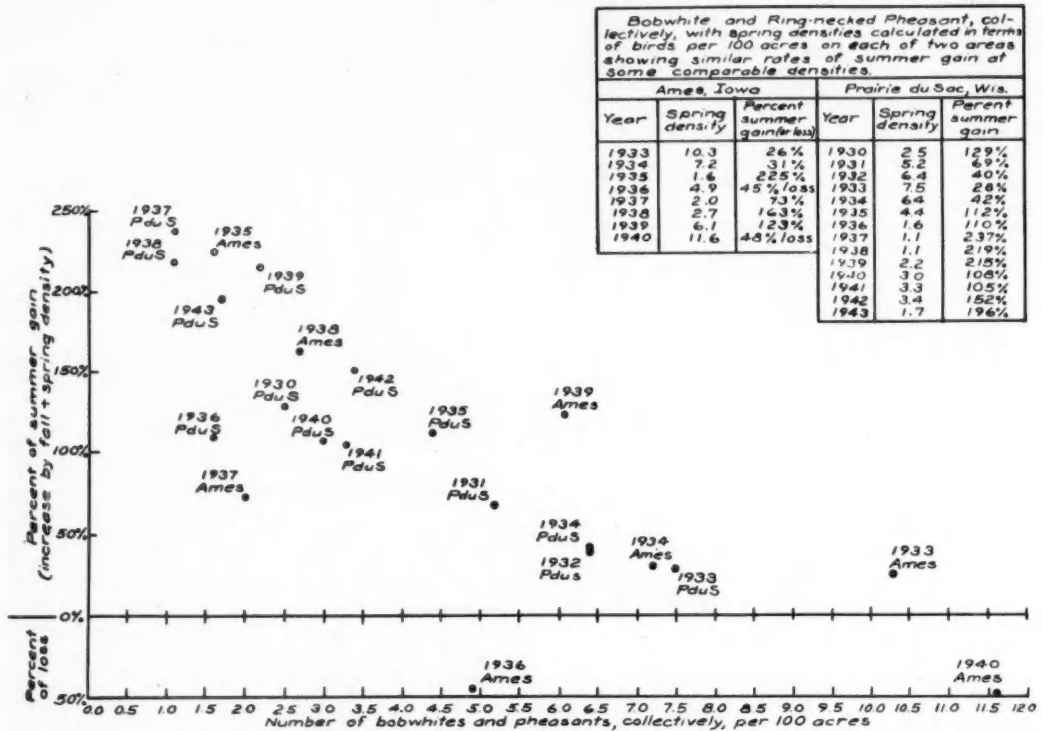


FIG. 22. Rates of summer gain (or loss) of mixed populations of bobwhites and ring-necked pheasants in relation to density on areas at Ames, Iowa, and Prairie du Sac, Wis. Data points from the two areas were plotted together chiefly in an effort to learn more about responses at high densities.

Phases I and II at Prairie du Sac seem almost as definite as the gear shift of an automobile. Ordinarily, the population was in one phase or the other or in what could be interpreted as in transition (i.e., in the winters of 1939-40 and 1942-43).

Summing up the evidence, I would say that the phase chronology of the area's bobwhites could defensibly be outlined as follows: phase I, winter of 1929-30; phase II, summer of 1930; phase I, for the winters of 1930-36 and for all of the intervening summers, a strong $5\frac{1}{2}$ years; phase III, summer of 1936 and at least the early part of the winter of 1936-37; phase I, summer of 1937 and winter of 1937-38; phase II, summer of 1938 and winter of 1938-39; phase I, summer of 1939 and part of the winter of 1939-40; then, about two years or perhaps a little longer of phase II, beginning some time in the winter of 1939-40 and continuing through the winter of 1941-42; phase I, summer of 1942 and part of the winter of 1942-43; finally, phase II, for an undetermined period.

In reviewing discrepancies between my versions of spring and fall data of Figures 5 and 6 and the values that Kabat obtained independently from Gastrow's journals, I recognized only one as having possibilities of changing the above phase assignments;

it might be that the summer of 1938 was in phase I instead of in phase II.

The gear-shift definiteness of the two principal phases at Prairie du Sac may not logically be ascribed to chance or to any of the usual biotic or climatic variations. Then, too, now that the pattern has been defined by the Prairie du Sac quail data, we can detect many signs of the same or similar phase effects in data for other areas and for other species. Despite much lack of synchrony in incidence of phases I and II for areas and species, there is surely more definiteness in the parts of curves indicated by data points of Figures 7-9 and 11-21, generally, than merely "happened"; with Prairie du Sac in mind, the reader may easily see even in single "off" points possible manifestations of phases that might be quite well defined by more complete data. At any rate, deficiencies notwithstanding, the existing data would seem to attest very well to the reality of the phases here described.

We admittedly have gone nearly as far into an inquiry of phase phenomena as the limitations of our knowledge permit. It becomes increasingly a temptation to postulate the operation of a master mechanism.

Examples of local differences in mortality or fecun-

dity from one cause or another multiply with each careful study that is made, but the net effects of so many of these differences are so often partially if not wholly cancelled out by intercompensatory trends that their roles as truly limiting factors become dubious, indeed.

The over-all dominance of the phases remains—density depression modified by what else?

As Elton wrote in his book on fluctuations of mouse-like rodents (13, p. 230), "So we are left . . . with a good many hints of some great cosmic oscillation, expressing itself in periodic upheavals in the biotic community, but we still lack the full key to the problem . . ." thus we also are left. And we likewise have grounds for concurring with Elton's thought that in time ". . . we may begin to understand this extraordinary oscillation, which I cannot help believing, will lead us back to very curious meteorological and perhaps astronomical processes. . . ."

The possible connection between sunspot cycles and animal fluctuations has been a subject of much attention (for a recent review, see 9, pp. 177-199), finally receiving from MacLulich's work on the snowshoe hare in Canada what looks like conclusive disproof (54, pp. 104-113). But might there not be relationships with things other than sunspots, which our current ignorance prevents us from recognizing?

The great majority of species of which I know that would seem to suffer predation or nonemergency losses most nearly in proportion to total numbers are invertebrates and lower vertebrates. Higher vertebrates, of kinds treated within this paper, suffer relatively more in proportion to numbers during their immature stages, but it can be readily seen, for example, that the Prairie du Sac bobwhites in phase I did not suffer even at immature stages at rates comparable to those for phase II and that phase III was accompanied by rates of nonemergency losses more in proportion to numbers than at any other time.

In Figure 23 are plotted, with reference to densities per 100 acres, all of the percentages of actual or computed nonemergency losses of low-mobility native Galliformes during phase III, or its judged equivalent, that I have been able to get together.

Rates of summer loss of bobwhites on different areas were computed on the same basis as the rate for Prairie du Sac (see Figure 10 and associated discussion). I make no claims for my figure of a 55% summer loss for the Connecticut Hill grouse except that it is the best that I could arrive at from the data published by Edminster (12, pp. 826, 831, and errata slips); it is probably too conservative.

The points of Figure 23 do not line up well enough to encourage curve-fitting, but, assuming that the summer loss rate at Connecticut Hill was materially higher than I computed, we have only one point (for southern Iowa) that departs radically from the trend shown by the others.

We see, then, what seems to be a general tendency of nonemergency loss rates during the low of the

cycle to be a function of density, *per se*, young birds or old, summer or winter.

What the cyclic depression may do, in effect, is to nullify the advantages higher vertebrates at low to moderate densities usually enjoy by virtue of their superior ability to take care of themselves, individually. Protection normally afforded by thresholds seems to be greatly lessened at such times.

In other words, during phases of maximum depression, we may see, with respect to relatively scarce higher vertebrates, the most literal realization of the thesis of proportional predation of McAtee and others (55). The mere fact that losses may not be due even largely to predation does not alter the fact of vulnerability; and the frequently observed interplay and superimposition of disease, weather emergencies, human interference, etc., should not outweigh evidences of lowered, collapsed, or suspended thresholds.

I am not sure that the phase phenomena of ruffed grouse and bobwhites are so very closely linked. The grouse data seemed to reflect a gradual tightening, a climax, then a relaxation of some adverse factor, but, within what may be judged to be particular phases, the species showed considerable uniformity in responding to density. The bobwhite, on the other hand, switched from phase to phase according to no rhythm that I can see, except in its lowest depression phase, which coincided with those of its own and other species over wide areas.

The many weather, environmental, nutritional, and disease hypotheses that have been put forward in explanation of animal cycles have, in my opinion, one common disqualification if applied to the phase phenomena that may be a primary attribute of such cycles. I do not see how they can account in any way whatever for the definiteness of responses in relation to density that are to be expected for given phases.

Computations as to probable nonemergency losses of low mobility native Galliformes, in northern United States at times thought to reflect greatest cyclic depression.

Area	Species	Summer loss rate indicated by "1" after year	Winter loss rate indicated by "2" after year	Initial density, birds per 100 acres	Rate of loss per approx. 135 days
Prairie du Sac, Wis.	Bobwhite	1936		6.5	49%
"	"	"	"	3.2	31%
Ames, Iowa	"	"	"	12.2	90%
Southern Iowa	"	"	"	12.1	21%
Seville Grove, Wis.	"	"	"	11.1	72%
"	"	"	"	3.1	29%
Hunt City, Ill.	"	"	"	3.8	9%
Connecticut Hill, N.Y.	Ruffed Grouse	"	"	22.6	38%
"	"	"	"	12.6	61%
Northcentral Minnesota	"	"	"	13.6	78%
"	"	"	"	7.7	50%

* See text for discussion of shortcomings and origin of figures.

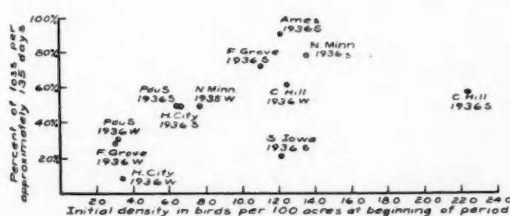


FIG. 23. Rates of nonemergency loss, actual and computed, of bobwhites and ruffed grouse in relation to density in areas of northern United States at or very near the low of the "game cycle."

The only alternative hypothesis that has so far appealed to me is one of a dominant agency bringing on depression phases through modification of ordinary limits of intraspecific toleration in the species affected. This, let it be confessed, is inspired more by largely unpublished data on the influence of changed intraspecific tolerance in muskrat populations than by any observations on Galliformes, but I have been unable to think of contrary facts that would rule out the broader application.

The validity of such a hypothesis is nevertheless conditioned by too many unknowns to warrant detailed exposition at this time. Quite possibly, it may not be the answer at all.

Thus, this paper closes on an unfinished job, on what can be but a preliminary treatment of the density factor that may so mightily dominate the course of populations. And it also closes in a way reminiscent of Pearl & Parker's (64, pp. 215-216) reference to "apparently another element . . . besides mere physical density, which element in our ignorance we may perhaps tentatively call psychological."

SUMMARY

A 15-year ecological study on an area of 4,500 acres near Prairie du Sac, Wis., was centered upon the bobwhite quail but also dealt with a number of associated species, especially other wild Galliformes, predators, and "buffers."

It was found that year-to-year differences in many of the conventionally regarded "limiting factors" had no perceptible influence on basic population trends. Although severe mortality frequently resulted from starvation and weather emergencies, and through the medium of predation, the outstandingly influential factor in the population mechanics of north-central states bobwhites was seen to be their own density relations as modified by what may be termed depression phases.

The data available from Prairie du Sac, other north-central areas, and the literature showed a very strong tendency for bobwhite population gains in a specific locality, spring to fall, to be in inverse ratio to spring densities. These rates of gain plotted against densities on coordinate paper tended to define reverse sigmoid curves, seemingly irrespective of most variations in temperature, rainfall, farming practices, and kinds and numbers of associated wild species, including predators.

Rates of summer gain of bobwhites in relation to density were subject to depression through the presence of introduced wild Galliformes (such as ring-necked pheasants, which, as bobwhite competitors, may be thought of somewhat in the sense of extra bobwhites); but the most pronounced depressions of summer gains occurred through the evident operation of the phases.

Similarly, the data showed a strong tendency for rates of nonemergency winter loss (including most loss from simple predation and from inter- and intra-specific adjustment) to follow mathematical patterns determined by density and phase effects. Wintering

populations experienced low rates of nonemergency loss and little if any acceleration of loss rates with rising densities as long as the populations remained below thresholds of security; but such loss rates for populations in excess of secure levels tended, when plotted against densities, to define characteristic sigmoid curves.

Inverse ratios in summer gains and operational levels of winter thresholds showed what looked like phase linkages.

Except for the summer of 1936 and the winter of 1936-37, Prairie du Sac bobwhite populations were responsive to two recognized phases, one of "normal" and the other of depressed rates of summer gain and correspondingly increased rates of nonemergency winter loss. Within the time-span of influence imposed by each phase, the above rates of gain or loss conformed to mathematical formulas with a high degree of predictability; but the time of changing of one phase to the other was not predictable according to any known criteria.

It would be premature to try to say just how closely the two main phases of the Prairie du Sac bobwhites may be identified with the general "game cycle" in the north-central region, but a third extreme phase appeared to be linked with extreme depressions (in 1936 and 1937) of nearly all of the region's mammals and birds about which information is available. In the case of the classically cyclic ruffed grouse, the lesser phase changes seemed to follow a more predictable course, one of progressive sequences as the low of the cycle was approached or passed.

Despite an apparent lack of synchrony and periodicity in the two main phases of the Prairie du Sac bobwhites and what would seem to be similar phases of this and other species elsewhere, the suggestion is made that depressed rates of summer gain and increased rates of winter loss in relation to density, if not clearly due to emergencies, may be more reliable indications of cyclic behavior than the often overstressed gross fluctuations in numbers of animals. This applies particularly to species that are highly susceptible to confusing emergency losses—as the bobwhite wintering in the northern parts of its geographic range.

Of the properties shown by the bobwhite and at least some other higher vertebrates during cyclic depressions, one may be judged significant: a tendency to suffer nonemergency losses more nearly in straight proportion to numbers than at other times.

No really satisfactory explanation for phase phenomena, periodic or otherwise, yet seems to be in sight. Current preference is expressed for some sort of cosmic influence possibly modifying the psychology (notably as concerns limits of intraspecific toleration) of the species affected.

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ECOLOGY AND MANAGEMENT OF THE REDHEAD,
NYROCA AMERICANA, IN IOWA

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TABLE OF CONTENTS

	PAGE
INTRODUCTION	37
METHODS OF RESEARCH.....	37
SPRING MIGRATION.....	39
Dates of Arrival and Departure.....	39
Numbers of Migrants.....	40
Redhead Associations During Migrations.....	41
Sex Ratios.....	41
NESTING	41
Pre-nesting Activities.....	41
Courtship and Mating.....	41
Movement Toward Nesting Territory from Courtship Grounds.....	42
Adult Bird Activities.....	42
Nesting Habitat Associates of the Redhead.....	42
Nesting Season.....	42
Breeding Populations and Nesting Densities.....	44
Fate of Nests and Eggs.....	44
Nest Destruction.....	45
Water Fluctuations.....	45
Predators	46
Nest Desertion.....	46
Eggs	47
The Clutch.....	47
Incubation	48
Covering for Eggs.....	49
Hatching	49
Renesting	49
Nest Construction.....	50
Nesting Cover.....	51
JUVENILE REARING.....	55
Rearing Cover.....	55
Juveniles on the Water.....	57
Brood Counts and Juvenile Mortality.....	58
FALL MIGRATION.....	60
Hunting	60
YEARLY PRODUCTIVITY.....	61
FOOD HABITS.....	62
MANAGEMENT PRACTICES IN RELATION TO THE REDHEAD.....	63
Environmental Conditions.....	64
Water Requirements.....	64
Area of Water Habitat Desirable for Nesting.....	64
Manipulation of the Water Level.....	65
Emergent Vegetation.....	65
Nesting Cover.....	65
Interspersion of Cover.....	66
Agricultural Practices in Relation to the Nesting Habitat.....	67
Rearing Areas.....	67
Food Plants.....	68
SUMMARY	68
LITERATURE CITED.....	69

ECOLOGY AND MANAGEMENT OF THE REDHEAD, *NYROCA AMERICANA*, IN IOWA

INTRODUCTION

Perhaps no other waterfowl species within recent years has decreased so rapidly or to such an extent as the redhead, *Nyroca americana*. Reduction in numbers has been brought about largely as the result of overshooting and destruction of nesting grounds through drainage and drought. The present breeding range includes chiefly large refuges in the western states and marsh areas in north-central Nebraska, northwest Iowa, the east half of North Dakota and South Dakota, a narrow strip on the western edge of Minnesota, southern Manitoba, Saskatchewan and southwest Alberta.

An investigation of certain diving ducks in Iowa was begun in March, 1938, to obtain life history and ecological information applicable to progressive waterfowl management practices. Upon completion of a preliminary survey, the redhead was chosen as the species for intensive investigation. The research was confined mostly to about 9 square miles of lakes, marshes and potholes in Clay and Palo Alto counties in northwest Iowa, known as the "Ruthven Area" (Fig. 1). The acreages of water and ownership are listed in Table 1.

For counsel and encouragement I am deeply grateful to Dr. Carl J. Drake, Dr. George O. Hendrickson, and Dr. Paul L. Errington, all of the Department of Zoology and Entomology, Iowa State College, and to Dr. Thomas G. Scott, Leader, Iowa Cooperative Wildlife Research Unit. For assistance in identification of plants I am indebted to Dr. Ada Hayden, Department of Botany at Iowa State College.

TABLE 1. Water areas of the Ruthven Area.

State Owned	Size (acres)	Depth (feet)	Privately Owned	Size (acres)	Depth (feet)
Lost Island Lake...	1260	12-16	Mud Lake.....	460	1-4
East Mud Lake....	160	0-3	Smith's Slough....	117	1-3
Round Lake.....	450	2-4	Barringer's Slough..	700	1-4
Trumbull Lake....	1190	4-6			
Elk Lake.....	261	4-6			
Virgin Lake.....	200	2-8			
Barringer's Slough	500	1-4			
Dewey's Pasture					
potholes.....	103	0-3			
Dan Green's					
Slough.....	285	3-6			

Redheads were recorded as nesting in 1885 (Cook 1888) at Clear Lake, Cerro Gordo County, then the most southern breeding record in Iowa. In 1889 redheads were reported only as spring and fall migrants (Keyes & Williams 1889) and in 1907 it was doubtful that redheads nested in Iowa (Anderson 1907). DuMont (1933) quoted Bennett as having observed nesting redheads, and Bennett (1938) reported 22 redhead nests found in Clay and Palo Alto counties, 1932-37.

METHODS OF RESEARCH

Observations were made at the Ruthven area from March 20 to August 30, 1938, March 20 to December 1, 1939, and March 20 to September 5, 1940. In addition to week-end trips to the area in 1938, fall migrations of redheads and other ducks were observed at Goose Lake, Hamilton County, Iowa. Hunting conditions and records of kill of redheads were secured in 1939 on the area, and in 1938 additional kill records were obtained at Goose Lake.

To facilitate nesting and vegetation studies, aerial photographs of the Ruthven area, prepared by the United States Department of Agriculture, were secured.

It was necessary to search the emergent vegetation of the sloughs and marshes to secure information on the nesting habits. The nesting territory was checked weekly for additional nests built during the week and to take data on nests already under observation. To find efficiently a maximum number of nests a procedure of passing over the marshes and potholes in a definite systematic manner was followed. The factors having a bearing on the readiness with which females flushed which indicated the possible location of nests were: (a) time of day, (b) strength of the wind, (c) degree to which incubation had advanced, and (d) temperature at the time of observation. Usually the females flushed several hundred yards from the observer after swimming a considerable distance from the nest before flying. To get as near as possible to nest sites before the females flushed, the potholes with little or no open water were traversed from the leeward at intervals of 5-10 yards, and a slight wind generally was helpful in the search for nests.

On small water-filled potholes and small plant-covered bays of the lakes, the edge of the vegetation next to the open water was searched first to prevent disturbed incubating ducks swimming from their nests to open water before flushing.

Wind-blown down feathers were sought as signs of nests. This method of locating nests was most useful for approximately the first three weeks of the nesting season or until about June 1, after which the down became increasingly scarce and "cotton" from cotton-wood trees (*Populus deltoides*) made the down difficult to distinguish at any great distance. Red-head down feathers in prairie marsh wren (*Telmato-dytes palustris dissaepus*) nests often indicated that a redhead nest was not far distant. Some nests were found by following paths made by muskrats (*Ondatra zibethicus*) through the dense vegetation. Nest searching was more successful in early morning and late afternoon than near mid-day.

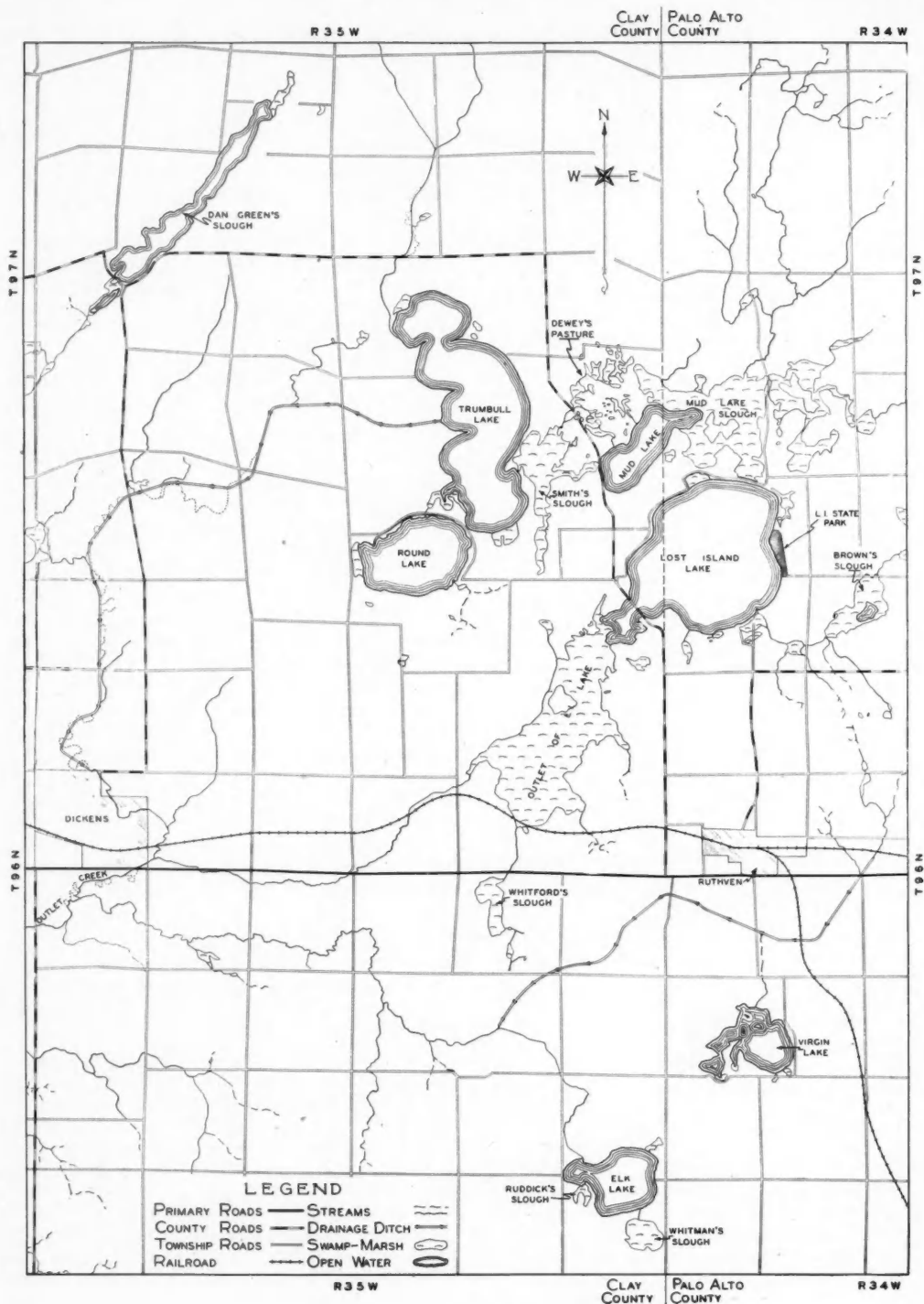


FIG. 1. The Ruthven Area.

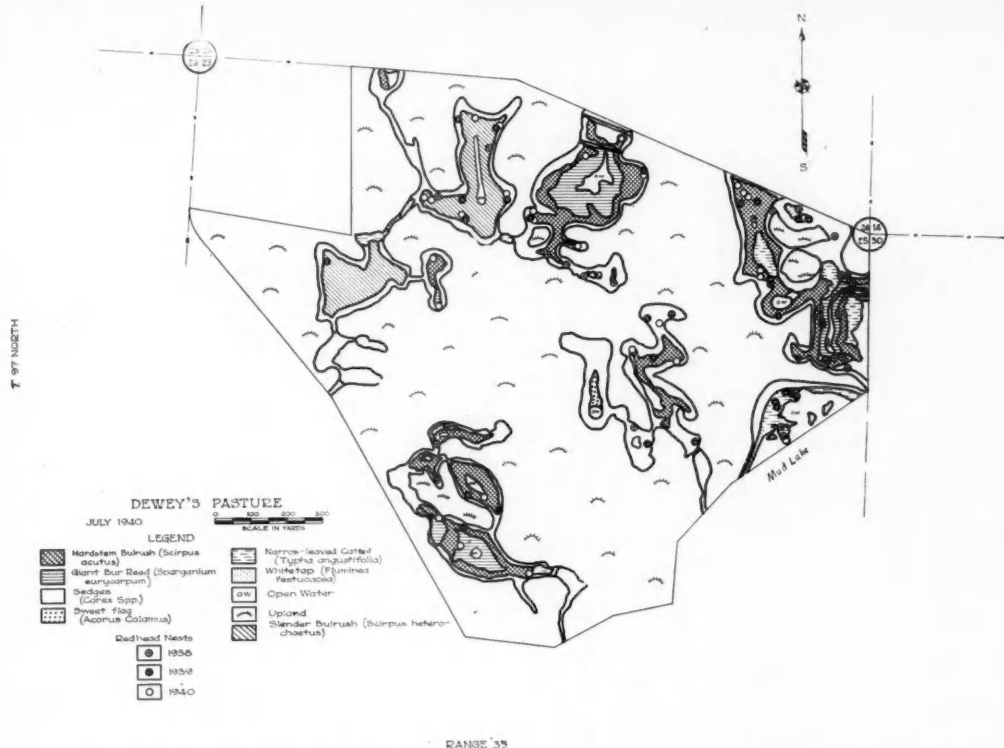


FIG. 2. Vegetative map of Dewey's Pasture showing locations of nests in relation to vegetation.

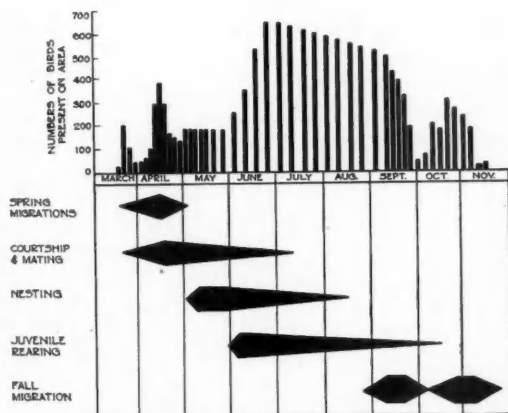


FIG. 3. Seasonal life history chart of the redhead in Iowa. Fall migration as indicated was broken into: (a) migration of young from the research area, and (b) migration of birds from the north.

SPRING MIGRATION

DATES OF ARRIVAL AND DEPARTURE

In the days of spring shooting prior to 1914 and when market hunting was at its height, the gunners and sportsmen from eastern cities planned on arriv-

ing at the lakes of northwest Iowa about March 20. Through experience they found that date to correspond closely with the arrival of the most desirable duck species: canvas-backs (*Nyroca valisineria*), redheads, lesser scaup ducks (*Nyroca affinis*), common mallards (*Anas platyrhynchos*) and American pintails (*Dafila acuta tzitzihua*).

The dates of arrival of the redheads, 1938-40, were respectively March 21, March 22, and March 21. The first ducks to reach the lakes, mallards and pintails, arrived about March 15. Of the diving ducks, the scaups arrived first, followed by the canvas-backs and American golden-eyes (*Glaucionetta clangula americana*). Ring-necked ducks (*Nyroca collaris*) and redheads came approximately the same time, while ruddy ducks (*Erismatura jamaicensis rubida*) and buffleheads (*Charitonetta albeola*) were not present until about two weeks later.

The principal spring flight of the redheads during the years under observation came April 11-18, 1938-40. Bennett (1938b) recorded April 8 as the date of main redhead spring flight in 1934. The spring flight covered approximately 45 days each spring (March 20 to May 5). Because some of the redheads remained to nest the date of the last migrants passing through the area could not be accurately determined. However, by the first week in May these

remaining behind began to seek the nesting habitats and no further decrease in numbers was noted.

NUMBERS OF MIGRANTS

From March 20 to May 5, 1938-40, the respective yearly numbers of observed migrant redheads were approximately 3,500, 4,750, and 3,000. Migrating redhead flocks not exceeding 25 individuals were the general rule, but as many as 110 redheads were observed feeding in a small pothole near Lost Island Lake at the height of migration.

The spring flight was broken into two distinct parts, the vanguard and the main flight. The numbers of redheads after March 21 or 22 dropped to a small portion of the vanguard number, but gradually increased again until the peak was reached about April 15. The numbers of birds present in 1940 were not in excess of one-half those during the preceding years, 1938 and 1939, until near the end of the flight. At the end of the 1940 spring flight numbers of redheads had increased until the nesting population was only slightly under the resident population of 1939.

In total numbers of spring migrants the redheads were exceeded by the common mallards, American pintails, baldpates (*Mareca americana*), blue-winged teals (*Querquedula discors*), shovellers (*Spatula clypeata*), ring-necked ducks and lesser scaup ducks. Fewer ruddy ducks, American golden-eyes, buffleheads and hooded mergansers (*Lophodytes cucullatus*) were noted than redheads. Gadwalls (*Chauliastur streperus*), green-winged teals (*Nettion carolinense*) and redheads were observed in approximately equal numbers.

The first migrant redhead into the Ruthven area found the lakes and sloughs solidly frozen over in 1940 but only partly frozen over in 1938 and 1939. Dates on which the ice left the large lakes and marshes varied as much as 18 days: March 21, 1938, March 26, 1939, and April 8, 1940. However, small shallow ponds and marshes cleared of ice several days before the larger lakes. A close correlation between the arrival of large numbers of redheads and other diving ducks and the permanent opening of the water was noted. Immediately after April 29, 1940, when the larger marshes thawed, an increase of all diving ducks was noted; no such correlation was seen in the early migration of the mallards, pintails, and gadwalls. Whereas the early migrant surface-feeding ducks frequented the cornfields during the period when the ponds were frozen, the diving ducks were dependent upon open water for food. After arriving most of the diving ducks including the redheads quickly deserted the lake region if open water was not found. Those few diving ducks remaining after the first days of arrival as well as many thousands of surface-feeding ducks sought small open springs at the exits of drainage tiles. During the cold weather periods, below 32° F., migrating redheads and other ducks flew and courted but little and fed sporadically. Normally the first available water areas were marshes bordered by closely grazed pastures where tramping cattle during the previous season had left

exposed muddy shore lines. Into these edges poured thousands of waterfowl at the first thaw of the season.

The preference of the majority of the redheads and other diving ducks for the water areas changed progressively as the ice cleared from shallow ponds to deeper lakes. Succession from shallow water to deeper water is indicated as follows: (a) Dewey's Pasture and other pasture potholes (0-3 ft. deep); (b) Barringer's Slough, Mud Lake (1-4 ft. deep); (c) Growing Pond (3-4 ft. deep); (d) Trumbull Lake (4-6 ft. deep); (e) Lost Island Lake (12-16 ft. deep).

Analysis of one of the favored feeding and day-resting sites of the Growing Pond disclosed a small 3-acre bay with water approximately 4 feet deep and surrounded by willows and cottonwoods on the east, west and south shores while the north side of the bay opened to the lake. Dry, dead, emergent vegetation of the previous season covered approximately 25 percent of the bay's water surface in the following proportions: (a) narrow-leaved cattail (*Typha angustifolia*), 20 percent; (b) hardstem bulrush (*Scirpus acutus*), 70 percent; (c) sand-bar willow (*Salix longifolia*), 10 percent. A survey of the submerged plants taken during July, 1939, showed coontail (*Ceratophyllum demersum*), sago pondweed (*Potamogeton pectinatus*), and bladderwort (*Utricularia vulgaris*) to dominate, while duckweeds (*Lemna minor*, *L. trisulca*, *Spirodela polyrhiza*) floated in colonies on top of the water.

In daytime, bays of large lakes and small sloughs and potholes within one-eighth mile of the larger lakes were utilized by redheads in feeding, resting, courting, and mating prior to nesting. At dusk, flocks of redheads left feeding and resting grounds of the day to spend the night in concentrations or rafts on the large open lakes, particularly Lost Island, Trumbull and Elk lakes. With the aid of a flashlight and a slow-running motorboat flocks of redheads as well as lesser scaups, ring-necked ducks, mallards, and pintails were observed on the lakes on several nights during the spring migration.

At dawn, and often just before, the redheads arose from the lakes either to travel on northward or to return to nearby feeding grounds for the day. A half-hour after dawn the flight from the night resting lakes to the feeding sites was completed.

The middle of the day was spent resting. The redheads normally rested upon the water, although they had no aversion to resting upon muskrat lodges, matted vegetation, floating logs, and boards or other material above the surface of the water.

The redheads were often found in coves and near high banks during severe, cold windstorms, although it was not uncommon for the birds to remain on the open lakes and ride the waves for long periods of time. In periods of abnormally cold weather the ducks often sought emergent vegetation: dense stands of hardstem bulrush, river bulrush (*Scirpus fluviatilis*), narrow-leaved cattail, reed grass (*Phragmites maximus*) and burreed (*Sparganium eurycarpum*). No redhead casualties attributed to cold weather were

found although American coot (*Fulica americana americana*) and smaller water birds suffered greatly.

Early morning concentrations of diving ducks on lakes where none was present the night before suggested that night was the principal time of flight for migrating redheads. Not all migrating flight took place at night, for redheads were observed flying into Barringer's Slough and Mud Lake at all hours of the day.

REDHEAD ASSOCIATIONS DURING MIGRATIONS

During the height of spring migration the redheads traveled in flocks predominantly of its own species, with lesser scaup ducks and ring-necked ducks almost invariably included. In the early stages of migration, March 20-April 1, and toward the end of the flight, April 15-May 1, almost every conceivable combination of diving duck species was seen flying together. Baldpates and gadwalls often were observed feeding on plant scraps brought to the surface of the water by feeding redheads.

SEX RATIOS

Of a total 3,400 redhead sexed on the spring migrations, 1,999 were males and 1,401 were females, a ratio of 1.42 males to 1 female. With the exception of the ruddy ducks the numbers of redhead males to females were more nearly equal than in any of the other diving ducks.

TABLE 2. Sex ratios of redheads during spring migrations. Figures in parentheses refer to the numbers of migrants counted for the sex ratios.

1938 Male to Female	1939 Male to Female	1940 Male to Female	3-year total Male to Female
1.45 : 1 (511 : 303)	1.43 : 1 (1050 : 743)	1.23 : 1 (438 : 355)	1.42 : 1 (1999 : 1401)

NESTING

PRE-NESTING ACTIVITIES

Courtship and Mating

The seasonal performance carried out by the redheads in choosing mates begins far south of Iowa, probably on the wintering grounds prior to starting north in spring. Since redheads begin to acquire their winter and nuptial plumage in December (Bent 1923), the reproductive stimulus probably begins at that time. By the time the redheads reached northwest Iowa (March 21) courtship was part of the daily routine, and the performance became more ardent as the date of nesting approached.

Although the sex ratio was about 1.5 males to 1 female, there were almost invariably two or more males to each courted female because some of the females were resting or feeding short distances away from those in courtship. By April 25, 66 percent of the redheads were estimated as paired. Females not mated by this date were attended by an increasing number of males, as high as six, which apparently had left other mated females. Toward the end of

the courtship period, May 10 to 15, small flocks of unmated males occasionally were seen flying over marsh and lake. Later, May 20 to June 10, as the mated males deserted the incubating females, the flocks contained as high as 30 drakes. After July 20 no males were in evidence. Although it is conceivable that they were hiding in the dense vegetation, it was thought that they moved out of the region to some unknown destination prior to molting. In Manitoba, Canada, male redheads move from the nesting habitat to the center of large lakes to acquire their eclipse plumage (Hochbaum 1939).

The sex ratios of the redheads taken during the late courtship and early nesting season, May 1-30, gave a sex ratio of 1.14 males to 1 female. The sex ratio of 118 redheads in the duck nesting habitats of the Prince Albert District, central Saskatchewan, Canada, was 1.12 males to 1 female (Furniss 1935, 1938).

Courtship activities, primarily display and pursuit by the males, are often returned by the females. The males within a group attempted to gain favor with the female by bowing, by sudden jerking of the head, or by throwing the head far over the back toward the tail. Little courting was done in the air, and males flying after females over the marshes often attempted to force the females to alight. The male, usually flying behind the female, generally alighted on the water first. Courtship was most active for 2 to 2.5 hours after dawn and in the evening for 1.5 to 2 hours before dark.

The voice of the female was loud and coarse at times, quiet at other times. The soft voice described as "*queh que-e-eh*" (Wetmore 1920) was heard more often during the early days of courtship. From males with open mouths, no sound other than a slight hiss was heard.

The selection of the mate was made before copulation took place, and all observed instances of copulation took place apart from the group of ducks. On April 19, 1940, at 5:30 a.m. a group of eight redheads was observed feeding in the southwest bay of Growing Pond. After feeding for 15 minutes one pair drifted away from the rest. The female led the way and the male followed within three or four inches, swimming slowly. When 75 yards from the other ducks, the male seized hold of feathers at the base of the female's skull, overtook and covered her. The female was completely submerged, the male partially, during the 15 seconds required to copulate. Both birds ruffled their feathers and preened themselves for about 5 minutes before flying away.

Courtship activities appeared to be stimulated greatly by the presence of more than one pair of birds. Courtship was very seldom observed when a pair was alone, but the usual activity of feeding and resting of the lone pair was almost invariably turned to courtship when other redheads, males or females, joined the couple. The increased courtship activities of such concentrations were noticed not only during the regular pre-nesting season but through June, the

main nesting season. Decreased courtship activities were noted in redheads exposed to cold north winds, cloudy and stormy days, particularly during April.

Movement Toward Nesting Territory From Courtship Grounds

With the completion of mating, approximately April 20-May 5, larger water areas used prior to nesting were gradually deserted as the birds sought small potholes and marshes to nest. Nesting areas were shallow water basins with 18 inches or less water and dense emergent vegetation. Although courting continued in the nesting habitat, by the end of April locating a nest was the principal activity.

Not much time was spent in flying over the prospective nesting habitats. After several trips across a given marsh the birds alighted and explored the marsh from the water. Sometimes a number of sloughs and potholes was inspected before one was chosen. Sometimes a pair sought a nest site together. Females that were selecting nesting sites were often flushed from the dense nesting cover, while the males flushed from the open water of the waiting territory 50 to 100 yards away. Selection of nest sites was made early in morning and in the evening. When the birds began to frequent the nesting habitats, but before the nesting commenced, they returned nightly to the large open lakes to rest.

Adult Bird Activities

With the start of the nest, the companionship between the paired redheads began to wane. Prior to and several days after a nest was started and some of the eggs laid the male closely attended the female as he stood guard against intrusion of other of the species on the open water or on an old muskrat lodge near the nest. The male, usually flushed before the female, often flew over or near the nest site, presumably to warn her. In the small sloughs the flight of the male was carefully watched for he often disclosed the approximate position of the nest or of his mate. Whether he gave a signal call was not determined, but the mouth often was observed to open while the bird was in flight. The disturbed female if given time swam a short distance from her nest before flushing. The guarding role of the male was short-lived for he soon lost interest in the incubating female to join others of his sex. However, he responded to the call of the female for a few days after leaving her for a male frequently rose from a group of males to fly with the disturbed female.

The redhead was not found to be an aggressive bird and only occasionally fought or drove other birds away. Coots and baldpates were often not molested when feeding upon the particles of food dislodged from the bottom by feeding redheads, although other surface-feeding ducks, scaups and ring-necked ducks were driven away frequently. During migration, however, diving ducks fed and rested together with no visible friction.

Redheads appeared to be tolerant of other nesting water birds. Successful coot and pied-billed grebe

(*Podilymbus podiceps podiceps*) nests were found within a foot and ruddy duck and mallard nests were found within five yards of redhead nests. American coots often rebuilt abandoned redhead nests to rest on or lay eggs in, and ruddy ducks used old redhead nests as nesting sites. Rockwell (1911) noted two redhead nests within two feet of each other on a muskrat lodge. The closest redhead nests during the present study were six feet apart, one of which was deserted at the time of discovery.

The manner in which the females approached the nest varied considerably, but the usual method was to swim to the nest from the open patch of water within their waiting territory. The males usually remained on this open water, either sitting quietly on the water or climbing on a muskrat lodge. Two examples of redheads approaching their nests after flying from the feeding grounds on a large lake were observed. In one instance the female dropped into the water near her nest while the male continued flying around, finally alighting 100 yards away. Two males observed flying with a female over a nest site in a small marsh returned to a large lake one-quarter mile away, when the female alighted on a small open area of water 30 yards from the nest.

NESTING HABITAT ASSOCIATES OF THE REDHEAD

Birds of the marshes which nested and produced young within the nesting and rearing habitat of the redheads but which exerted no harmful effect upon that duck were: eared grebe (*Colymbus nigricollis californicus*), pied-billed grebe, eastern green heron (*Butorides virescens virescens*), black-crowned night heron (*Nycticorax nycticorax hoactli*), American bittern (*Botaurus lentiginosus*), eastern least bittern (*Ixobrychus exilis exilis*), mallard, gadwall, pintail, blue-winged teal, shoveller, canvas-back, lesser scaup, ruddy duck, marsh hawk (*Circus hudsonius*), king rail (*Rallus elegans elegans*), Virginia rail (*Rallus limicola limicola*), sora (*Porzana carolina*), Florida gallinule (*Gallinula chloropus cachinnans*), American coot, Wilson's phalarope (*Steganopus tricolor*), Franklin's gull (*Larus pipixcan*), Forster's tern (*Sterna forsteri*), black tern (*Chlidonias nigra surinamensis*), prairie marsh wren, short-billed marsh wren (*Cistothorus stellaris*), giant red-wing (*Agelaius phoeniceus arctolegus*), and yellow-headed blackbird (*Xanthocephalus xanthocephalus*).

NESTING SEASON

The 1940 nesting season of the redhead extended through 105 days, April 30 to August 12. In 1939 the season extended from May 1 to July 15, 76 days, and in 1938 from May 1 to July 16, 77 days.

The dates of nest construction followed the first warm weather late in April and early in May. The relationship between temperature and the dates of first nesting of the redhead is shown in Figure 4.

Twenty-two percent and 23 percent of the nests in 1938 and 1939 respectively were begun during the period of May 1 to 10, while only 11 percent in 1940 were begun in this period (Table 3). Subnormal

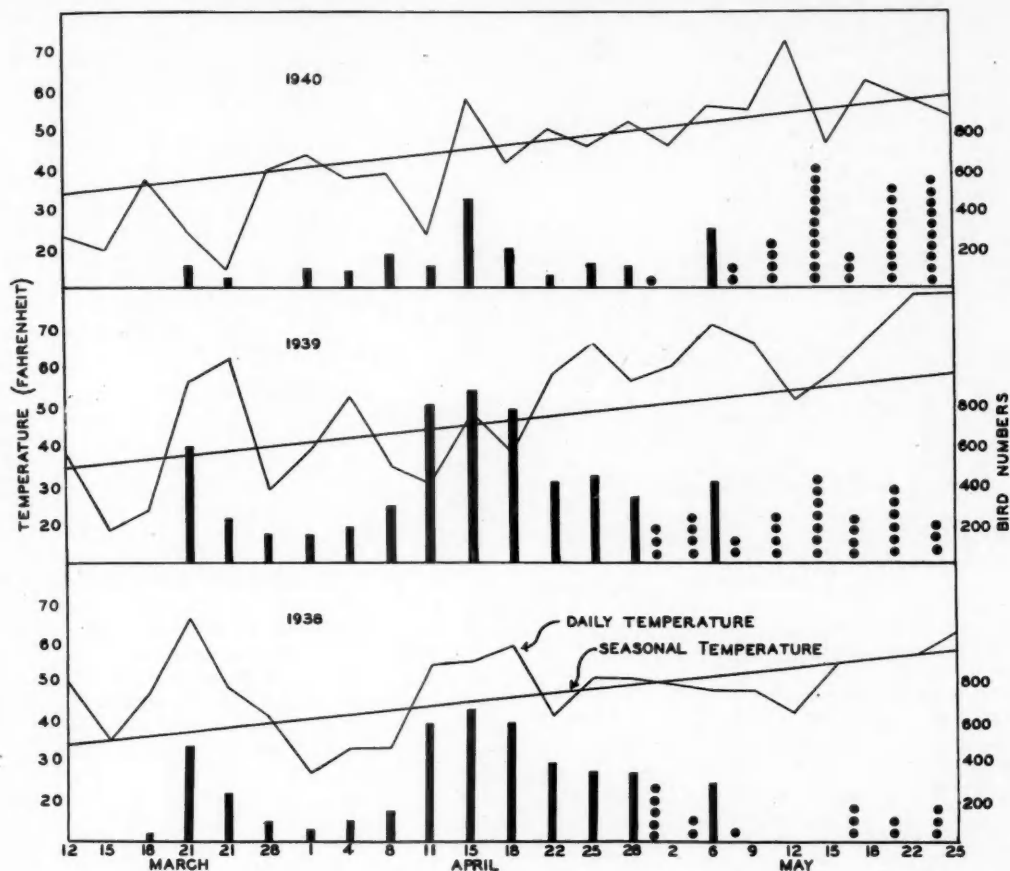


FIG. 4. Relationship of migration and start of egg-laying to temperature. Each dot represents start of a nest. Cold weather delayed the birds in migration and in egg-laying.

temperatures, excess precipitation and excess cloudy days characterized March and April, 1940 (Table 4). Late re-nesting attempts initiated after previous nests were unsuccessful extended the nesting season of 1940 more than four weeks longer than during the 1938 and 1939 seasons (Table 3) when nesting conditions were more favorable. Earliness of nesting was not affected by vegetative conditions because the nests were made in dead vegetation of the previous year. Slightly over 33 percent of all nests were constructed during the period May 10 to 20, and approximately 71 percent of the nests were started before June 1 (Table 3).

The largest number of nests, about 75 percent, were found shortly after the females began incubating the eggs, at which time the females flushed from the nests more readily than later. The distance which the females flushed from their nests varied with the stage in the incubation, climatic conditions, cover in which the nests were located, and manner of observer's approach. The female often flushed 25-50 yards

TABLE 3. Periods of nest initiation, failure and success of the redhead.

Date	Number of Nests Begun			Nest Failures			Nests Successful		
	1938	1939	1940	1938	1939	1940	1938	1939	1940
May 1-10..	8	11	6	..	1
May 11-20..	8	18	21	2	..	1
May 21-30..	7	9	13	..	4	6
June 1-10..	9	7	8	..	2	7	6	6	1
June 11-20..	5	2	2	3	1	9	5	12	9
June 21-30..	2	11	1	3	3	9	5
July 1-10..	6	3	3	8	7
July 11-20..	1	1	6	3	1
Aug. 1-10..	1	2
Aug. 11-20..	2
Totals...	37	47	59	16	9	31	23	38	27

or farther from the nest site, the distance depending on the interval that elapsed from the time the female left the nest until the observer approached near enough to flush her or until she had reached a place

TABLE 4. Pre-nesting season climatic conditions.

Date	Temperature (F°)			Precipitation (inches)			Number of cloudy days		
	1938	1939	1940	1938	1939	1940	1938	1939	1940
March.....	39.6	34.5	28.2	1.51	.57	1.49	9	6	19
April.....	49.0	46.7	45.5	2.89	1.20	3.58	9	5	14
Averages and totals.	44.3	40.6	36.8	4.40	1.77	5.07	18	11	33

from which flight could be made easily. No correlation was noted between the distance flushed and the time of day. Climatic factors, including the velocity of the wind, and the observer's approach to the nest with regard to wind direction were of more importance than the time of day. As incubation advanced the female flushed less easily from her nest. Females flushed from the nests or near the nests in 135 instances at an average of 35 yards from the observer with extremes of one yard and 250 yards.

BREEDING POPULATIONS AND NESTING DENSITIES

By approximately May 5 the migration was completed and the breeding population for the year was fairly constant. Census of the potential nesting population present in the research area May 5 and 6 in 1939 and 1940 is shown in Table 5.

TABLE 5. Census of potential nesting redheads, May 5 and 6, 1939 and 1940.

Area	1939 numbers	1940 numbers
Dewey's Pasture.....	27 pairs, 3 extra males	11 pairs
Barringer's Slough...	35 pairs, 9 extra males	52 pairs, 11 extra males
Smith's Slough.....	6 pairs.....	8 pairs, 2 extra males
Mud Lake.....	10 pairs.....	12 pairs
Lost Island Lake...	5 pairs, 2 extra males	10 pairs
Totals.....	83 pairs, 14 extra males	93 pairs, 13 extra males

Degree of efficiency in locating nests was extremely difficult to ascertain because of difficulty in searching all of the nesting cover and because of excellent concealment of nests. No one method was found satisfactory as a basis for determining the success of the search for nests. Three methods were used which gave indicative trends toward the nesting populations: (a) pre-nesting counts of paired birds in the breeding habitat, (b) thoroughness of the search, and (c) count of duck broods.

The pre-nesting count of the paired birds was most important in the evaluation of the percentage of nests found. The thoroughness of the search for nests indicated only what numbers of nests might be expected to be found on an area, considering the time put forth to find them. Counts of the broods which totaled 114 distinct broods for the 3 years were used as a supplementary check on the first two methods.

With the above methods it was estimated that approximately 60 percent of the nests were found during the study. A total of 160 nests was located and histories determined over the three-year period. On

the 5,700 acres of water in the research area only about 925 acres (16 percent) held aquatic vegetation dense enough for nesting redheads. The average yearly nesting density for the entire area was 1 nest to 66 acres or 1 nest to 11 acres of available nesting vegetation.

In Dewey's Pasture a series of five large potholes totaling 103 acres of available nesting cover held one nest to three acres, although densities approached one nest to two acres on three of the individual potholes, which is less than some on refuges of western United States (Kalmbach 1938; Salyer 1934; Williams & Marshall 1938). The nesting density for Dewey's Pasture did not vary greatly during different years of the study, whereas other marshes varied 75 to 90 percent in numbers of nests.

FATE OF NESTS AND EGGS

The successful completion of a nest depended upon a chain of unbroken events, extending over a period from the date of first egg-laying to the time the ducklings left the nest. Successfully terminated nests outnumbered unsuccessful nests (Fig. 5). Intervention of predators, abnormal climatic disturbances and human interferences brought unsuccessful conclusions to many nests. In a review of the literature on nesting success of waterfowl and other game birds Kalmbach (1939) considered as good an average success of 63 percent based on histories of more than 7,600 duck nests under varied conditions and stated that 70 percent would be a reasonable objective on managed areas. A hatching success of only 26 percent was reported on the Bear River Refuge, Utah (Williams & Marshall 1938) while in Iowa (Bennett 1938) a 40.5 percent egg hatch was reported. From 1,516 eggs in 150 nests during the present study, 45 percent (683 eggs) hatched successfully. The yearly success varied considerably with the conditions of the season. In the three years, 1938-40, about 55 percent, 74 percent and 43 percent, respectively, of the nests terminated successfully (Table 6). The success of the nests was considerably above the success of the eggs with the exception of the 1939 season. The relatively greater success of small clutches of eggs and the partial hatch of some nests which were considered successfully terminated were given credit for this. It was observed repeatedly that larger clutches of eggs in nests were destroyed or deserted in periods of distress (as in flood waters) while smaller clutches were saved from flooding.

As shown in Table 7, the dates when the clutches were begun as based on the laying of the first egg was at its peak May 11-20. The peak dates of nest initiation for the three years did not vary a great deal, although in 1940 nest-building and egg-laying were prolonged into July by the successive destruction of nests. The amount of nest destruction in 1939 over the entire season was slight, more or less uniform throughout, and no correlation was noted between dates of beginning and destruction of nests. The first peaks in new nest destruction in 1938 and



FIG. 5. Yearly success of redhead nests.

in 1940 were followed by secondary peaks in new nest building and egg-laying. After the high flood of June 29, 1938, which destroyed 11 nests, no new nests were started. By this date incubation was well advanced in all the nests under observation. Males had long before deserted the females and it is highly probable that the females were not in condition to begin reneesting at this late date. The peak of suc-

TABLE 6. Fates of redhead nests.

Year	Nests under observation	Nests terminated successfully	Percentage of successful nests	Nests terminated unsuccessfully	Percentage of unsuccessful nests
1938...	42	23	54.8	19	45.2
1939...	53	39	73.6	14	26.4
1940...	65	28	43.1	37	46.9
Totals.	160	90	56.2	70	43.7

cessful nests came three weeks after this period of greatest nest destruction. There was not sufficient time for the females of destroyed nests to reneest and bring off a brood. Also the males apparently were not available to females at this late date.

The interval between the peaks in nest destruction

TABLE 7. Loss and partial success of redhead clutches, 1938-1940.

Nests on which complete data were secured			
Dates on which clutches began	Number of clutches	Successful clutches	Failed clutches
May 1-10.....	25	17	8
May 11-20.....	47	30	17
May 21-31.....	29	19	10
June 1-10.....	24	13	11
June 11-20.....	9	5	4
June 21-30.....	2	1	1
July 1-10.....	6	2	4
July 11-20.....	1	1	..
Totals.....	143	88	55

and secondary peaks in nest starting was approximately 20 days. Since most of the peaks in nest destruction occurred late in the season when incubation ordinarily was well advanced, it appeared that the time required for most females to resume laying was about 15 to 20 days. Data from nests destroyed earlier in incubation or before the clutches were completed indicated a shorter time interval in which laying was resumed.

NEST DESTRUCTION

For convenience of discussion the fate of the unsuccessful nests and eggs may be given under two headings: (a) nest destruction, and (b) nest desertion. Of the 160 nests under observation 22 nests (14 percent) were destroyed and 48 nests (30 percent) were deserted (Fig. 6).

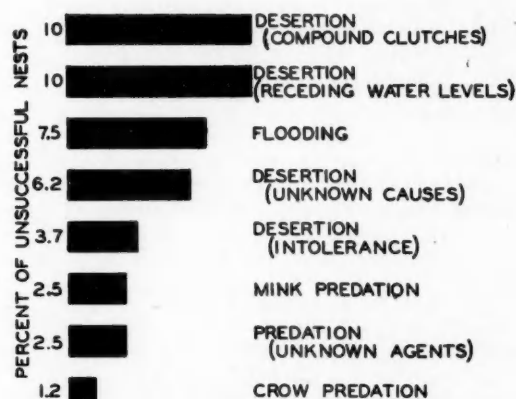


FIG. 6. Causes of redhead nesting failure, 1938-1940.

Redhead nesting was not directly affected by hay mowing operations, burning or grazing. Water levels favorable to redhead production were not conducive to any of these practices. Cattle in pastures around the edges of the marshes did not enter the larger sloughs to any extent. No grazing was permitted on Dewey's Pasture, which contained a group of small shallow ponds. Nests were not endangered by the limited cutting of wild hay around the edges of marshes because the marsh vegetation was not cut where the water was several inches deep. Burning of marshland was not a common practice and as a result no serious damage was caused to redhead nesting habitats. During two years of the study small patches of marshland too dry for redhead nesting were burned.

Water Fluctuations

The destructive animals so commonly associated with land-nesting duck species were largely eliminated from consideration because the water over which the redhead nested rendered the nests practically inaccessible to terrestrial predators. The location of the nest over water, however, was not always to the advantage of the ducks for often adverse climatic

conditions made this nesting site unstable, and unfavorable weather was the greatest single cause of nest destruction, chiefly by affecting the water level within the nesting habitat. Actual flooding of the nests accounted for 12 (20.6 percent) of the destroyed nests. On June 29, 1938, at the height of the nesting season a 4-inch rain, which fell in several hours, raised the water in potholes and slough-nesting sites from 6 to 18 inches and flooded 28 percent of the nests under observation. The 1939 and 1940 seasons were free from excessive amounts of precipitation and flooding was not a cause of nest destruction. Aside from the climatic factors the causes of nest destruction were few. Since the water over which nests were built excluded terrestrial predators, the avian and aquatic or semi-aquatic predators were the only types capable of inflicting damage. Predation on nests exposed by receding water levels often occurred after the nest had been deserted by the female.

Predators

The plains garter-snake (*Thamnophis radix radix*) and the red-barred garter-snake (*Thamnophis sirtalis parietalis*) frequented the marshes but no evidence was found to indicate that these snakes were predators on redhead eggs or juveniles. Examination of several snakes with bulging stomachs during the nesting season revealed that the snakes had gorged themselves on tadpoles and small frogs abundant at that season.

Turtles were not considered as nest predators, although some evidence was obtained which indicated that the snapping turtle (*Chelydra serpentina*) was a minor predator of juveniles. In April, 1939, 25 dead snapping turtles were found on the shore of an important juvenile rearing area, the Growing Pond, apparently victims of a disease. Virgin Lake also had a heavy population of snapping turtles, but it rarely raised a brood of ducklings. The other two turtles, the very abundant Bell's painted turtle (*Chrysemys picta bellii*) and the relatively scarce Blanding's turtle (*Emys blandingii*) were not found to be destructive.

The only bird recorded as destructive was the eastern crow (*Corvus brachyrhynchos brachyrhynchos*) which destroyed two nests (1.2 percent), one in 1938 and one in 1939. Exposed nature of these two nests rendered them easy prey to the crow. The number of crows was greatest early in spring, probably when they were migrating north while nesting crow population was relatively low. Many eggs of the ducks dropped promiscuously on the shores or elsewhere in the early nesting season were devoured by crows. No evidence was found of crows molesting redhead juveniles. Great horned owl (*Bubo virginianus virginianus*), short-eared owl (*Asio flammeus flammeus*), and marsh hawk (*Circus hudsonius*) were present in the area but were not known to be responsible for redhead nest losses.

Although no direct evidence was noted to indicate the species of predator responsible at four of the unsuccessful nests, the common mink (*Mustela vison*)

left hair, tooth marks on the eggs and seats sufficient in four nests (2.5 percent) to definitely attach the plundering to that animal.

The native mammals with the exception of the mink and muskrat did not have access to the redhead nests built over the water. Other mammals which may have been responsible for a small amount of predation on nests exposed by receding water levels were the thirteen-striped ground squirrels (*Citellus tridecemlineatus*), Franklin ground squirrels (*Citellus franklini*), coyotes (*Canis latrans*), red fox (*Vulpes regalis*), long-tailed weasels (*Mustela frenata*), Bonaparte weasels (*Mustela cicognanii cicognanii*), striped skunks (*Mephitis mephitis*), spotted skunks (*Spilogale interrupta*), American badgers (*Taxidea taxus*), domestic dogs (*Canis familiaris*) and domestic cats (*Felis domestica*).

Nest Desertion

Females deserted 30 percent (48 nests) of the total nests under observation. Nests were abandoned most frequently during the laying and early incubation period, but some nests were deserted several days before the eggs were to have hatched.

The recession of the water level during the dry season of 1940 proved a greater cause of nest failure than the flood waters of 1938. The desirability of redhead nesting cover having certain water depths was recognized early in the investigation. No nests were built on land, although nests were found by the writer and others on the land at the Bear River Refuge, Utah, an area of heavy concentrations of nesting ducks. During the 1940 season 14 nests (21.5 percent) left on dry land by the receding water level were deserted. The relatively stable water level of 1939 proved to be most satisfactory as shown by the 73.6 percent hatch as compared to the 54.8 percent hatch in 1938 and 43.1 percent in 1940. Deserted nests kept under observation during the entire season showed some nests were not molested for two or three months, but eggs in other nests were destroyed by predators shortly after the nests were deserted.

Another factor responsible for unsuccessful nests was the intolerance of the nesting females toward other females or disturbance from ducks other than the rightful owners laying in the nests. The compound clutches, which usually occurred early in the season, represented the laying, in addition to the rightful owner, of one or more females, probably before their nests were constructed or following an earlier nesting failure. Sixteen nests (33.3 percent of the deserted nests) were deserted apparently because of compound clutches, while six other nests were deserted because of the apparent intolerance of the redheads for the eggs of other species of birds. Whether the compound clutches were incubated or not depended on the date in the history of the nest when the parasitic eggs were deposited. Parasitic eggs laid in nests late in incubation increased the chances of nest failure, while in some of the nests eggs deposited simultaneously with the rightful owners' eggs were hatched successfully.

Table 8 indicates the correlation between the nesting success and the number of compound clutches within the species and between the redheads and other species. The 1939 season was remarkably free of compound clutches. As shown, water levels which have a direct bearing on nest failure or success in general (items 8-9) closely correlate with the degree of promiscuous laying. When the water level rose or receded rapidly the amount of promiscuous laying increased greatly. Redheads, ruddy ducks, mallards, pintails, coots and American bitterns laid eggs in each others' nests.

TABLE 8. Egg parasitism in the nesting of the redhead.

	1938	1939	1940
1. Redhead nests parasitized by other redheads.	2	0	12
2. Redhead eggs in parasitized nests.....	35	5	72
3. Average number redhead eggs per parasitized nest....	5.8	5	12
4. Average number redhead eggs in unparasitized nests.....	8.4	9.9	10.3
5. Redhead nests parasitized by other duck species.....	6	1	6
6. Other ducks' eggs in redhead nests.....	13 Ruddy Duck	4 Ruddy Duck	6 Ruddy Duck 7 Pintail
7. Other ducks' nests parasitized by redheads.....	4	0	8
8. Water levels...	Raised during nesting season	Stationary during nesting season	Receded during nesting season
9. Success of redhead nests.....	54.8	73.6	43.1

During 1938 when the water level raised during the nesting season, resulting in flooded and destroyed nests, eight redhead nests were parasitized by redheads and other duck species, notably ruddy ducks. One compound clutch was found in 1939, when the water level remained practically stationary. In 1940, when the water level receded 15-18 inches in favored nesting habitats, 15 nests were parasitized by other ducks' eggs. A similar correlation was noted between the number of nests of other duck species parasitized by redheads and the stability of the water level. These nests in which redheads laid included 10 ruddy ducks, one mallard nest and one American bittern nest. An American bittern nest was found with a week-old bittern and two redhead eggs, one of which was hatching at the time.

Eggs

Eggs and egg shells found late in April on muskrat houses, matted emergent vegetation and other resting sites were evidence that laying often began before nests were constructed. Because the redhead spent

most of the time on the water, relatively few pre-nesting eggs were found and most of those found had been broken and the contents eaten by crows.

After May 1 the laying corresponded closely with the dates of nest building and similar factors influenced both. The normal laying period began May 1 and extended to approximately June 10-15, after which re-nesting attempts extended the date of laying about to July 15.

The Clutch

Clutch size in the successful redhead nests varied from four in late re-nesting attempts to 19 eggs in compound clutches (Fig. 7). A maximum of 23

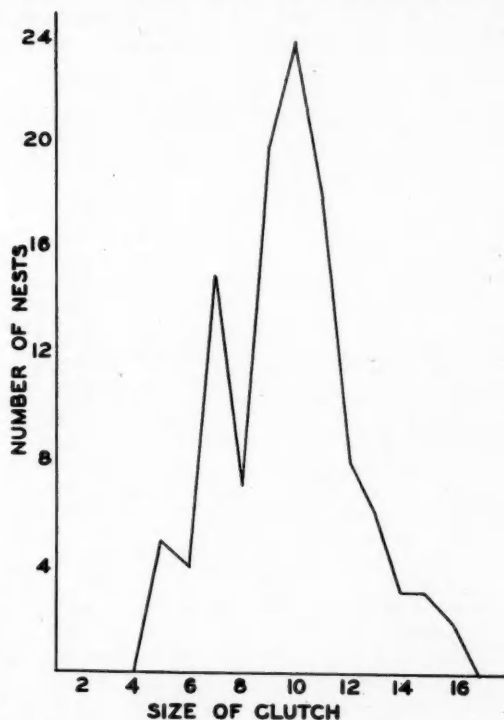


FIG. 7. Complete redhead clutch size frequencies.

eggs in one compound clutch was not incubated. The average size was greatest at the beginning of the season and tapered off as the season advanced, although some slight unaccountable variations occurred during the season. An average of 9.75 eggs to a nest was recorded for 115 complete redhead nests during the three seasons. The yearly average number of eggs to a nest was 10 in 1938, 9.21 in 1939 and 10.08 in 1940. An average of 11.1 eggs to a nest was recorded in 1940 for 41 complete clutches excluding the re-nesting attempts which averaged 6.6 eggs to a nest. A large percent of the nests containing 15 eggs or more resulted from two females laying in one nest. Nests started during the period May 11-31 contained the largest number of eggs to a nest. The

parasitic eggs along with some or all of the other eggs were often pushed from the nest by the female redhead and another clutch started.

Forty-five percent of the eggs produced young. Favorable climatic conditions of 1939 resulted in a 70.8 percent egg hatch while in 1940 only 33.3 percent of the eggs hatched. Numbers of undeveloped eggs were relatively small (4.7 percent of eggs), the majority representing single eggs left in otherwise successful nests. In one instance nine of 11 eggs were found undeveloped, probably infertile, in a nest May 15, although in general there was no seasonal concentration of these undeveloped eggs.

All fertile eggs did not hatch at the same time and those embryos that remained in the nest when the female led away the hatched ducklings apparently died of exposure. A total of 83 eggs (5.5 percent) containing dead embryos in various degrees of development were found in nests. Undoubtedly many of these late-hatching eggs were laid at various times in the history of the nest by females other than the incubating female. Flooding and predation accounted for 644 (42.5 percent) of the unsuccessful eggs while the fate of 35 eggs (2.3 percent) was not determined. No significant difference was noted in numbers of undeveloped or dead embryos during the three seasons of study.

TABLE 9. Size of redhead eggs.

Period and Condition	Average number of eggs per nest	Number of clutches measured	Average Length x Width (mm)
Total period.....	9.75	48	60.2 x 43.4
May.....	10.25	32	59.52 x 43.29
June-July.....	8.5	12	61.26 x 42.51
Late-nests June-July.....	7.25	4	56.90 x 41.90
Parasitic redhead eggs.....	59.50 x 42.53
Undeveloped eggs.....	59.53 x 41.73

TABLE 10. Size of complete redhead clutches and numbers of young hatched to a successful nest, 1938-1940.

Date clutches began	Data on complete clutches		Hatching success		
	Complete clutches	Average number eggs per clutch	Number of successful clutches	Total number eggs hatched	Average young per clutch
May 1-10..	23	10	16	132 of 168	8.2
May 11-20..	40	10.5	31	263 of 334	8.5
May 21-31..	24	10.7	17	134 of 168	7.9
June 1-10..	19	8.8	11	96 of 103	8.6
June 11-20..	8	8.2	4	28 of 33	7.0
June 21-30..	2	7	1	9 of 9	9.0
July 1-10..	5	6	1	5 of 6	5.0
July 11-20..	1	6	1	1 of 6	1.0
Totals and averages...	122	8.8	82	667 of 827	8.1

Measurements of 237 eggs ranged from extremes of 50.6 to 66.5 millimeters in length and from 39 to 46.6 millimeters in width. The average egg measured 60.2 x 43.4 millimeters (Table 9). Variations in length

amounted to 15.9 mm. or 26 percent of the medium; widths varied 6.6 mm. or 15 percent of the medium. The largest egg measured 66.5 x 56.6 mm. while the shortest was 50.6 x 43.8 mm. One small egg, 14 x 32 mm., found in a complete clutch, was far out of range of ordinary variation. No significant difference was noted between the size of the eggs laid at different times during the main nesting season, although the size of eggs in four re-nesting attempts averaged somewhat less than the medium (Table 9).

Incubation

Incubation usually began within 24-48 hours after the last egg was laid. Instances of hatching over a three- or four-day period indicated that incubation might have occasionally begun prior to the laying of the last egg, but in other nests evidence such as finding freshly laid eggs throughout the incubation period indicated parasitism by other redheads. The nest was usually well filled with eggs at the time incubation began.

The female's devotion to the clutch increased with the addition of eggs and the progress of incubation. The first eggs were usually laid before the nest was finished. A maximum of one egg was deposited each day by the female, but rarely was this rate maintained over the entire laying period. Generally one to three days more than the number of eggs were required to complete the clutch. The eggs were not attended during the interval of laying, although the female generally stayed in the same slough or marsh within several hundred yards of the nest. However, flight was not limited for often frightened females flew two or three miles before alighting.

The time of day that the eggs were deposited was not the same for all the females. Although few on this point, the data gathered indicated that egg deposition took place at any hour of the day. In two closely watched nests, however, egg deposition took place between 11 a.m. and 1 p.m. in one nest, and between 7 and 7:30 p.m. in the other.

The incubation of the eggs was accomplished by the females alone. To record the periods of day the females were on and off the nest, a machine was developed with modifications from the itograph (Kendeigh & Baldwin 1930). It was made by running a measured tape by use of a clock past an activated electrical relay equipped with a pencil which in turn was attached with wire to the entrance of the nest. Contact which was made during an exit or entrance to the nest was recorded on the tape. Records were made at four nests, one from three days after incubation started to several days after hatching while on the others records were made from two to 17 days during incubation. Three were initial nests and one was a re-nesting attempt.

No definite rhythm of incubation was detected in the redheads as rest periods away from the nest came at irregular intervals during the day and night. Unlike the blue-winged teal as reported by Bennett (1938a) which left the nest for food and rest but

twice daily, the incubating redheads left as many as 26 times and in no instances fewer than 3 times (average 6) during a single 24-hour period. An average of 17.5 hours a day were spent incubating, but only 9.6 hours during the 16 hours of daylight were spent on the nest. Prevailing temperatures determined, in part, the amount of time spent in incubation by the redheads. During extremely hot days the females often were on the nests for intervals of one or two minutes at a time. Females remained relatively close to the nests during the night, but occasionally they left the nests for an hour or two and absences of several minutes duration were not infrequent.

The female of the renesting attempt spent fewer hours incubating and left the nest more frequently than did the females on the initial nests. Warmer weather was probably responsible in part at least for this difference. Data on one of the initial nests and on the renesting attempt are given in Table 11.

TABLE 11. Incubation periods of an initial nest and on a renesting attempt.

Type Nest	Times females left nests per day			Hours per day spent incubating eggs	Hours of sunlight (16 hrs.) spent on nest	Hours of night (8 hrs.) spent on nest	Average degrees F. temp.
	Max.	Min.	Av.				
Initial	10	3	5	17.06	9.59	7.47	69.4°
Renest.	26	3	8	14.97	8.51	6.46	76.7°

The incubation period of the redhead has been given as 28 days by Job (1915) and Bertgold (1917), and as 22, 23 or 24 days by Bent (1923). The period from the peak of nesting construction to the peak of hatching was four weeks, which may indicate approximately 30 days as the period for laying plus incubation. Six nests, the activities of two of which were recorded by machine, found before incubation began and revisited at the time of hatching, had an incubation period of 24 days for five clutches and 28 days for one clutch.

Covering for Eggs

The covering for the eggs consisted of down feathers mixed with small pieces of vegetation to form a loose blanket around the rim of the nest which could be easily pulled over the eggs. The amount of down in the nests varied with individual nests and with certain periods in the history of the same nest. Down feathers were added several days before incubation began but were most profuse two to four days after incubation started. Wind, prairie marsh wrens and short-billed marsh wrens were responsible for the disappearance of down from redhead nests. As incubation advanced down feathers became scarcer until the majority of the nests contained only a few feathers at the time of hatching. However, the amount of small, loose stalks of vegetation held together by down feathers was increased to cover the eggs and to compensate for the decreased down feathers. Occa-

sionally nests were observed which had extremely little or no down during the entire period of incubation.

TABLE 12. Down feathers lining redhead nests. Based on complete clutches at the time of greatest abundance of down in nests.

Year	Number nests with profuse down	Number nests with medium down	Number nests with scarce down	Number nests with no down
1938.....	5	7	8	5
1939.....	20	10	9	2
1940.....	8	25	16	1
Totals.....	33	42	33	8

Whether the eggs were covered or not when the female left the nest was noted at weekly observations of each nest throughout the incubation period. A female when flushed from her nest very seldom covered the eggs. Nests from which the females were known to be absent without having been flushed by the writer showed well concealed eggs.

Hatching

The earliest date of hatching was June 1 and the latest August 12, a period of 73 days. Eggs in 57 percent of the nests hatched within the 3-week period, June 8 to 30.

The chipping period was about 16-18 hours. Of 4 eggs under observation, two required 16 hours, one 17 and the fourth 18 hours for chipping. The shell cap was not pushed off until the egg had been chipped three-fourths the way around. Egg teeth remained on the ducklings 30-36 hours after hatching.

Within two hours after hatching the juveniles had dried, their down was fluffy and shedding small white scales. The egg shell, with the exception of the cap and small particles which were crushed along with the fluffy blanket of down and vegetation into the bottom of the nest, was generally pushed into the water. The presence of circular egg caps near the nest and the covering of the eggs which were smashed into the bottom of the hatched nests were used as criteria to distinguish hatched from destroyed nests.

Three mortality factors not discussed under nesting failures are yet to be considered. Several instances of unsuccessful hatching resulted when the egg shell of one hatched juvenile slipped over the end of an unhatched egg. Four juveniles which hatched after the females had deserted the nests died from exposure. Observed mortality from natural defects were very few during the study. One club-footed juvenile was found in a renesting attempt and the remaining three eggs in the nest were undeveloped.

RENESTING

Undoubtedly renesting attempts were begun shortly after the first nests were destroyed or deserted in the early part of the season. However, because of the

difficulties involved in distinguishing these early re-nesting attempts only those late nests definitely known to be renests are here presented. Decreased clutch size, poor construction of nests, and lateness in the season were the principal criteria used in distinguishing such late re-nesting attempts from initial trials. Table 13 summarizes the data on late re-nesting attempts, of which 16 were found. Numbers of renests recognized as such increased with the number of initial nest failures. Thus, in 1940 when initial nest failures were highest the largest numbers of re-nesting attempts were found. Nest failures in 1940 were distributed rather evenly throughout the season. Whether or not this uniform nesting failure throughout the season kept the birds in a physiological condition to lay late in the season cannot be said. However, it is interesting that no re-nesting attempts were made after 11 nests were destroyed (flooded) late in the nesting season, June 29, 1938.

The average number of eggs in known re-nesting attempts was 7.26 as contrasted to 9.75 for initial nests. Eggs in ten (62.5 percent) of the re-nesting attempts hatched.

TABLE 13. Data on late re-nesting attempts.

Year	Successful	Failure	Average number eggs per clutch
1938.....	3	1	8.25
1939.....	3	0	7.67
1940.....	4	5	6.66
Totals or average...	10	6	7.25

The first nest definitely distinguished as a re-nesting attempt was found June 1, and the last re-nesting attempt hatched on August 12. The part which re-nesting plays in the final productivity of the redhead is discussed in the section on annual productivity of the species.

NEST CONSTRUCTION

Construction of nests was often begun two or three days to a week before egg-laying started. Though loosely woven and large enough to hold four or five eggs at first, the nests were built stronger and larger as laying proceeded until shortly prior to incubation the nests reached full proportions.

Nests were built entirely by the females. Often the nests had no foundations other than the stalks of the plants on which the nest was built, but more frequently, even though the nests were constructed in dense plant growth, the foundations extended down to the bottom.

The vegetation which was used as materials for construction of the nests was gathered within two or three yards of the nest sites. The nests were usually built of the plant species in which the nests were located. Ninety-five percent of the nests were built of only one plant species. Although as many as 12 different plants were recorded as nesting materials, no more than five plants were used in the construction of any one nest.

The first nests were constructed largely of dead vegetation of the previous year. The amount of green material used increased as the season advanced until the re-nesting attempts late in the season were made largely of green plants. Even though some of the nests were made of green plants the nests invariably had a lining of dry vegetation. Not until about June 1, before which 62 percent of the nests were built, was the current year's vegetation advanced enough to be used by the redheads in nest building. Greater quantities of green narrow-leaved cattail were used than any other green nesting material.

The redheads as well as other marsh nesting waterfowl were continually confronted with nests sinking because of the settling and decomposition of the under parts of the nests. Fresh materials were added frequently to the nests to keep the eggs above water. Rapid rises in water levels following sudden heavy rainstorms compelled the ducks to add materials very quickly to the nests and continue to do so until the highest water level was reached. Nests well concealed and protected by dense vegetation were often exposed following a heavy rainstorm during which the female ducks incorporated the surrounding vegetation into the nests. Nests built of the coarse-leaved plants such as bulrushes, cattails and reed grass were much more successful in avoiding flood waters than those constructed of the fine-leaved sedges. Bulrush appeared to be the most successful plant for such emergencies.

Table 14 presents the data on details of nest site in relation to water and land.

TABLE 14. Details of nest construction.

Year	No. nests	Distance to open water from nest site (yards)			Distance to upland from nest site (yards)			Water depth at nest site (inches)			Top of nest above bottom of the nesting habitat (inches)		
		Min.	Max.	Av.	Min.	Max.	Av.	Min.	Max.	Av.	Min.	Max.	Av.
1938..	42	1.0	250	61	5	250	74	2	34	15.4	11	49	22.6
1939..	53	1.0	250	36	2	200	52	0	18	9.1	4	31	16.8
1940..	65	0.3	100	31	3	250	88	3	27	8.6	6	36	16.0

The 9.1 inches of water selected by nesting ducks in 1939 were thought to represent a favored depth since the water level in that year was fairly stationary during the period of nesting.

Nests were built 9 to 23 inches in outside diameter, an average of 16.2 inches. Diameters of the inside or bowl of the nest were 5 to 10 inches, with an average of 7.5 inches.

The redhead in common with some other marsh birds constructed overhead coverings or cupolas for their nests. Cupolas were of two kinds. Either the nests were so placed that dense vegetation naturally overtopped the nests or the birds bent the surrounding vegetation into coverings. Forty-nine percent of the nests were equipped with cupolas. Approximately 65 percent of the nests had a ramp or runway con-

structed of coarse vegetation from the top of the nest into the water.

The nests averaged 28 yards from muskrat lodges, which for 64 percent of the nests was the nearest open water.

The materials for construction were generally small, broken or bent pieces of vegetation varying from a fraction of an inch to three or four feet long, depending on the species of plant, with an average of six to nine inches. The nesting cover chosen often determined the materials and the size of materials used in the nests. For example, plants such as cattail, bulrush and burreed furnished the largest pieces of nesting materials.

A circular nest was the general rule, though an occasional nest a few inches longer one way than another was noted. Nest building materials were usually placed in a circular or semi-circular form. The bottoms of the nest bowls were packed hard with fine plant materials. Nests and eggs were kept clean.

The size of the nests in general was conditioned by the depth of the water or the nest site and the plant species chosen for nesting materials. One nest of hardstem bulrush weighed 232 grams.

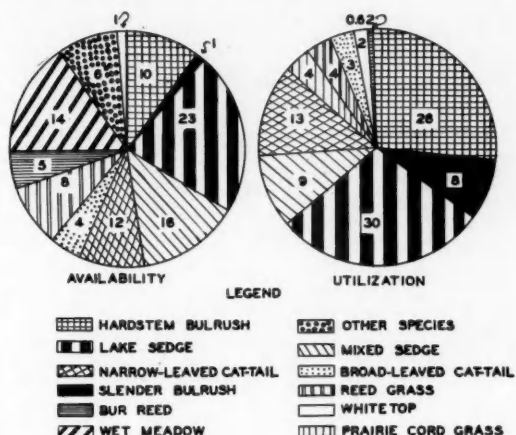
NESTING COVER

The essentials of a nesting habitat were the presence of emergent vegetation of desirable density, proper interspersed of cover and water, and a convenient water depth over the marsh bottom. Other minor, though essential, considerations in the evaluation of nesting cover were the nearness of cover to the rearing and feeding areas, availability of the cover during the nesting season, success of the nests in the types of cover, and the size of the habitat (Fig. 8).

Within the 5,800 acres of marshes, lakes and sloughs of the research area approximately 925 acres (16.2 percent) of emergent vegetation were available to the redheads for nesting. Although this vegetation grew in rather definite zones and had specific habitat requirements, mixtures of two or more plants were not uncommon. Nests were designated as occurring in the dominant cover species in which they were located.

The most extensive plant cover species was lake sedge (*Carex lacustris*) followed by narrow-leaved cattail, hardstem bulrush, and awned sedge (*Carex atherodes*). In addition to these species nine other minor plants of which the most abundant was reed grass made up the remainder of the cover (Table 15).

Nesting densities in the different cover species varied from one nest to two acres to as low as one nest to 45 acres. Hardstem bulrush carried one nest to seven acres, lake sedge one nest to 13 acres and narrow-leaved cattail one nest to 16 acres. Though of limited acreage, the slender bulrush (*Scirpus heterochaetus*) averaged one nest to three acres and whitetop (*Fluminea festucacea*) held one nest to 11 acres. One nest was located in the fraction of an acre of available cord grass.



FIGURES ARE PERCENTAGES

Fig. 8. Availability and use made of nesting cover by redheads, 1938-1940.

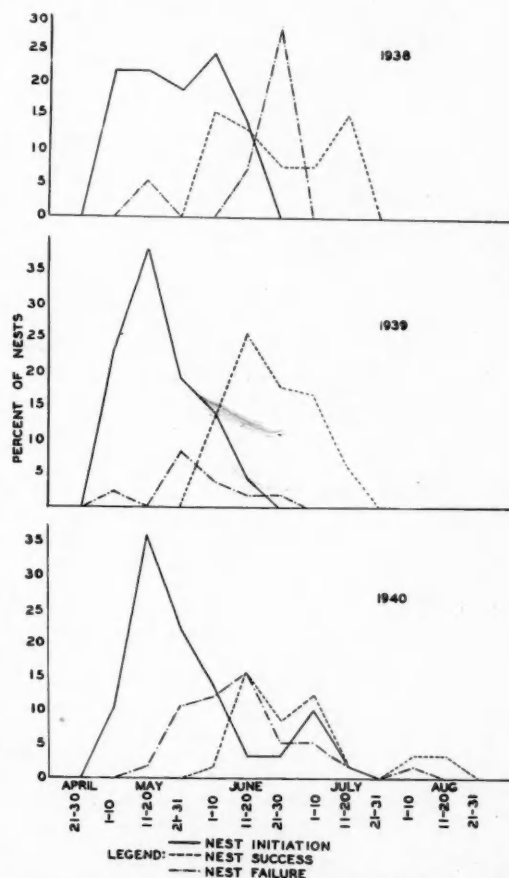


Fig. 9. Initiation, success and failure of redhead nests. Renesting in 1940 was responsible for the late nest hatching and failure.



FIG. 10. Muskrat lodge in common cattail. Redheads utilized such lodges as resting and sunning sites.

A concept of the relative values of cover types for nesting may be obtained by the use of a percent acreage-use ratio (Williams & Marshall 1938) which holds that the value of a certain plant cover is conditioned to a large extent by the amount available and the use made of it. Thus, based upon the ratio $\frac{\text{percentage acreage of a cover}}{\text{percentage acreage of cover}}$, the index values of the plants were found to range from 5.8 for slender bulrush to 0.4 for reed grass (Table 16). Small acreages and relatively small numbers of nests in some of the minor plants greatly exaggerated their true value as nesting cover. The fact that the hardstem bulrush had a nesting density of twice as many nests per acre as either sedges or cattails and that the value given it by the percent acreage-use ratio was higher showed that this bulrush and slender bulrush had greater attraction to the birds than the other types of cover.

Another factor which had a bearing on the value of a plant species as nesting cover was the success of the clutches in that particular nesting cover. Thus, it was found that in 1939 the choice of cover made little difference on the success of the nests. In 1938, however, when water levels rose rapidly nests located in sedges were invariably flooded, while in 1940 when water levels declined the percentage of successful nests was greatest in sedges and least in bulrushes. As pointed out earlier in the discussion of nesting success, the three important species of sedges produced a higher percentage of successful nests than did the two species of bulrushes. Thus, a cover plant may have seasonal values on unmanaged nesting habitats.

Ninety percent of the nests was constructed in marshes, sloughs and potholes, while only 10 percent was in the vegetation on the edges of the open-water lakes. The plant species in which the redheads nested appeared to be largely determined by the depth of the water at the beginning of the nesting season and by proper interspersed and density of cover, rather than a preference for a plant species itself.

TABLE 15. Nesting in relation to available cover.

Plant species	Acres of each cover type	Percentage of nesting area	Acres of cover per nest	Percentage of total nests found in each cover type	Total nests
Hardstem bulrush..... (<i>Scirpus acutus</i>)	94.2	10.1	6.7	26.3	42
Slender bulrush..... (<i>Scirpus heterochaetus</i>)	12.9	1.4	3.0	8.1	13
Lake sedge..... (<i>Carex lacustris</i>)	213.4	23.0	13.3	30.0	48
Awed sedge..... (<i>Carex atherodes</i>)	92.2	10.0	25.1	6.9	11
Water sedge..... (<i>Carex aquatilis</i>)	45.4	5.0	45.4	1.9	3
Beaked sedge..... (<i>Carex rostrata</i>)	14.8	1.5	0.6	1
Reed grass..... (<i>Phragmites maximus</i>)	78.1	8.4	39.0	3.8	6
Burreed..... (<i>Sparganium eurycarpum</i>)	52.7	5.7	22.9	4.4	7
Narrow-leaved cattail..... (<i>Typha angustifolia</i>)	116.1	12.5	16.6	13.1	21
Common cattail..... (<i>Typha latifolia</i>)	39.8	4.3	30.6	2.5	4
Whitetop..... (<i>Fluminea festuacea</i>)	11.8	1.3	11.8	1.9	3
Prairie cord grass..... (<i>Spartina pectinata</i>)	0.2	0.6	1
Rushes—spike rushes..... (<i>Juncus-Eleocharis</i>)	129.8	13.9
Sweet flag..... (<i>Acorus Calamus</i>)	11.6	1.3
Softstem bulrush..... (<i>Scirpus validus</i>)	4.9	0.4
Willows..... (<i>Salix</i> spp.)	8.0	0.9

TABLE 16. Evaluation of 10 leading nesting cover types.

Cover Type	Percent Acreage—use indices	Cover Type	Percent Acreage—use indices
Slender bulrush.....	5.8	Awed sedge.....	0.7
Hardstem bulrush...	2.6	Common cattail.....	0.6
Lake sedge.....	1.3	Reed grass.....	0.4
Narrow-leaved cattail	1.0	Water sedge.....	0.4
Burreed.....	0.8	Beaked sedge.....	0.4

Fluctuation of the water level may affect the vegetation used as nesting cover in several ways. An abnormally high water level may cover some of the low growing sedges near the shores, but in so doing more vegetation higher on the shore is made available. Use of this newly acquired cover is seasonal and use can be expected only until the vegetation changes in response to the new water level. However, a receding water level has a different effect upon the cover. Water receding from an area because of lower precipitation or drainage leaves good cover unavailable near the shores, thus decreasing the amount of nesting cover for the redheads and ruddy ducks. A change over a number of years in the den-

sity of a nesting cover type from abnormal water fluctuations may render a valuable nesting cover useless. A drop of 18 inches in the water depth practically eliminated as nesting cover the three most important cover plants (bulrush, sedge, and cattail) from Smith's Slough in 1940. Cattails were not used in 1940 in Dewey's Pasture after the water receded and left them dry, although they were important in 1938 and 1939 when the water level was high.



FIG. 11. Typical redhead nest constructed of hard-stem bulrush, with eggs pipping.



FIG. 12. Hills and labyrinth of sloughs in Dewey's Pasture. (Photo by Ada Hayden.)

Interspersion of the nesting cover with small areas of open water was one of the most decisive factors that determined the distribution of nests and the degree of utilization of nesting cover. Large blocks of dense cover have long been known to have a low wildlife productive capacity. The significance of this was brought out in the present study. Proper interspersion of cover and open water to attain a maximum utilization of the habitat was considered essential. Areas of open water within the cover had several important functions, one of which was to increase the edge effect. Since 85 percent of the redhead nests were situated within 50 yards of open water, the value of small clearings in the blocks of solid cover readily became apparent. The open water areas were chosen as bases for nesting operations. These openings performed, at least in part, the function of a territory were used by the females as areas upon which to alight before going to the nests, by the males as waiting areas while the females constructed nests and laid eggs, and by the pair as feeding grounds or as places from which to fly when alarmed or leaving the nesting area to feed. As contrasted to the surface-feeding ducks which are capable of leaving the water on a very steep incline the redheads and other diving ducks usually require a larger area from which to take to the air. The normal procedure for the redhead females was to swim to the open water area nearest the nest before flying. The size of the open water clearings used by the redheads in marsh and pothole nesting areas varied from a square rod to several acres in size, though the most frequently used clearing was three to four rods square. Over the marshes as a whole the nesting densities reached a maximum where not less than 10 percent and not more than 25 percent of the habitat was open water.

Whether these open water areas were artificial or natural clearings in the nesting habitat appeared to make little difference to the nesting waterfowl. Nests were conspicuously absent in large areas of nesting cover devoid of these openings in, for example, dense blocks of otherwise favorable nesting cover in East Mud Lake, and in the southeast corner of Barringer's Slough. Through activities in lodge construction, muskrats rendered large areas of cover favorable for redhead nesting by breaking up dense blocks of vegetation. Sixty-four percent of the ducks chose nesting sites in which the nearest open water was around muskrat lodges.

The plant species differed somewhat in the degree to which they were naturally broken up. Cattails and reed grass often died out in spots within dense stands of plants, and bulrushes in normal growths grew less dense than did sedges. Muskrats also showed a preference for cattails and bulrushes in which to construct their lodges.

From the foregoing discussion it can be seen how the redhead production on one marsh densely choked with vegetation might differ greatly from another in which the cover was interspersed with open water at intervals of approximately 100 yards.

One hundred and one nests (63 percent) were situated in dense vegetation, 55 (34 percent) in medium and only four (2 percent) in sparse vegetation. From 50-100 culms of bulrushes, 50-150 stalks of sedges or 8-18 stalks of cattails to 0.5 square meter were considered medium cover. Above these figures the cover was considered dense, while below the cover was considered sparse. Although nesting was mainly in cover considered dense, the birds avoided exceedingly heavy growths of vegetation. Success of the few nests located in the extra heavy vegetation was low. Of 29 nests in 1938 and 1940 located in bulrush 5 were located in very heavy vegetation exceeding 150 culms per square meter. Four (80 percent) were deserted or destroyed before completion of the incubation period. The nesting success of birds in extra heavy stands of cattails and sedges was similar to that in bulrushes but not so apparent.



FIG. 13. Juvenile redhead ducks just hatched. Nest of hardstem bulrush.

The size of the habitat also determined the degree to which it was used by redheads. Potholes under five acres separated from larger bodies of water by more than a quarter-mile were not used even though they contained the same cover species favored by the ducks in larger nesting areas.

The redheads showed a definite preference for the ends of sloughs and marshes as nesting sites. No particular difference was noted between the composition of the cover or the water depth in the ends as

contrasted to the sides of the same nesting habitats. Seventy-five percent of the redhead females chose to nest in the corners or ends of the marshes or lakes. This preference applied equally well to large and small areas.

There was no evidence to indicate that the distance from feeding areas was a factor in the selection of nest sites, since aquatic food plants were abundant within several hundred feet of any of the nesting cover.

Several instances of redheads being chased by coots, and vice versa, were noted during the pre-nesting period. The redheads were apparently tolerant of other of their kind and toward other species of birds, notably the ruddy duck, mallard, coot, Florida gallinule, and pied-billed grebe in the choice of nesting sites and young raising. Table 17 summarizes redhead nesting data for 1938-1940.



FIG. 14. Prairie kettle-hole, Dewey's Pasture. Soft-stem bulrush and river bulrush in center, tussock sedge near the edge bordered by a zone of spike rush. (Photo by Ada Hayden.)

TABLE 17. Summary of redhead nesting data, 1938-1940.

Principal vegetation in which the nests were located	Total nests		Unsuccessful nests		Total eggs		Hatched eggs		Undeveloped eggs		Embryos left in nests		Eggs in unsuccessful nests		Eggs unaccounted for	
	Total	Successful	Destroyed	Deserted	Total	Hatched	Undeveloped	Embryos	Left in	Unsuccessful	Eggs	Unaccounted	Eggs	Unaccounted	Eggs	for
Hardstem																
bulrush.....	42	23	5	14	395	188	11	22	172							
Slender bulrush..	13	5	1	7	116	31	4	7	69							5
Lake sedge.....	48	29	9	10	500	219	26	30	204							21
Awned sedge.....	11	8	1	2	111	68	2	6	35							..
Water sedge.....	3	2	..	1	21	11	1	1	8							..
Beaked sedge....	1	..	1	..	5	5							..
Reed grass.....	6	5	..	1	50	21	4	8	13							4
Burreed.....	7	2	3	2	59	16	3	..	40							..
Narrow-leaved																
cattail.....	21	12	2	7	176	96	8	9	60							3
Common cattail..	4	1	..	3	43	14	1	..	28							..
Whiteweed.....	3	2	..	1	28	8	10	..	10							..
Prairie cord grass.	1	1	12	11	1
Totals....	160	90	22	48	1516	683	71	83	644							35

*Total eggs in 150 nests.



FIG. 15. A flooded redhead nest in a dense stand of lake sedge.

JUVENILE REARING

REARING COVER

Juvenile redheads were reared on the larger semi-open marshes and lakes. Often the nesting cover also was utilized as rearing cover, but in general the cover plant species used by juveniles were less dense than nesting cover. Nesting cover was around the edges of the marshes where water depths of 12-15 inches and dense growth of cover plants prevailed, while the juveniles were reared in sparse to open cover where water depths ranged from 24 to 48 inches deep. Rarely were juveniles observed on the large open lakes, though several broods were observed on several successive days on Lost Island and Trumbull lakes. Lack of cover and possibly food on the deep lakes probably kept the broods from staying long on the open water. Broods seldom ventured over 50 yards from protective cover until they were four to six weeks old, and even at the age of six to eight weeks seldom were seen on the large bodies of open water except during favorable weather.

The small potholes and marshes were deserted by the females with their brood shortly after hatching, and the journey to larger lakes and marshes was undertaken. Broods hatched in the potholes of Dewey's Pasture were reared in Mud Lake, and those hatched in east Barringer's Slough were reared in the Growing Pond (Fig. 1).



FIG. 16. Redhead nesting cover on the edge and juvenile rearing cover in the center. (Photo by Ada Hayden.)



FIG. 17. Effect of livestock on marsh vegetation. Dense growth of smartweed where cattle are excluded. Slough near Lost Island Lake. (Photo by Ada Hayden.)

Because a less dense stand of vegetation was required for juvenile rearing than for nesting cover, the acreage of rearing habitat was several times that of nesting cover. As with the nesting cover, the water level determined to a large degree the amount of available juvenile rearing cover. Broods seldom or never left the water, and when the water level decreased the acreage available to the juveniles decreased proportionately.

Six fairly distinct types of rearing cover were present in the research area. The tall emergent plants served more frequently as cover than the short plants. Table 18 presents a summary of the plant communities in which broods were recorded.

1. Reed grass-Cattail Community.—Approximately 20 percent of all the emergent vegetation was composed of these plants. Because these plants were located in deeper water toward the centers of the marshes this community constituted approximately 50 percent of the total rearing cover. As high as 90 percent of the rearing cover of Barringer's Slough and the Growing Pond was composed of these plants.

TABLE 18. Juvenile rearing cover in Iowa.

Plant Communities	Total number of broods 1938, 1939, 1940	Cover Conditions	
		Approximate percent of total emergent vegetation	Approximate percent of total emergent cover available to juveniles
1. Reed grass—cattail.... (Hardstem bulrush occasionally. Dense to open stands with small open water areas).	168	20	50
2. Hardstem bulrush—river bulrush—burreed. (Open sparse to medium dense stands with small clearings.)	93	40	40
3. Sedges—sweet flag—burreed..... (Localized areas of broad-leaved cattail.)	7	35	5
4. Slender bulrush—burreed..... (Open to dense stands.)	..	3	3
5. Sedges—spike rush—whiteweed.....	7	1.5	1
6. Willow.....	10	0.5	1
Totals.....	285	100	100

A water depth of 18-40 inches was common for this type of cover, and in the water at the bases of the plants submerged aquatic food plants grew. In the Growing Pond cattails were greatly reduced as a result of an increase in water depth from a 36- to a 44-inch depth. Fifty-eight percent of the broods were observed in this plant community.

2. Hardstem bulrush-River bulrush-Burreed Community.—Over the entire area this cover type was most widespread and was next in importance to the reed grass-cattail cover. Mud Lake and Smith's Slough each had approximately 90 percent of the cover composed of this plant community. The sparse stands of hardstem bulrush and river bulrush too thin for nesting were readily utilized by juveniles. Approximately 40 percent of the cover was of this type, and 33 percent of the broods were reared therein. In general this type cover grew best in water 12-18 inches deep, although these plants were observed in 48 inches of water. Bulrushes rarely grew on the damp soil at edges of the lakes; this drier zone was well occupied by sedges.

3. Sedges-Sweet flag-Burreed Community.—This cover type constituted the outer edges of the rearing cover. Sedges predominated and were composed of lake sedge, awned sedge, water sedge, and beaked sedge. Although the sedges constituted approximately 35 percent of the total emergent vegetation, the water depths in which the sedges grew limited their usage to only about 5 percent of the rearing cover. Seven broods (2.5 percent) were observed in this community. A water depth from 6 to 15 inches predominated in this cover type during the juvenile rearing period. The heavy density of the plants and the shallow water characteristic of most sedges apparently were unattractive to redhead broods.

4. Slender bulrush-Burreed Community.—This represented about three percent of the total cover, and had limited use as juvenile rearing cover, although it was important as nesting cover. Water depth varied from 12 to 24 inches, but the densest growth



FIG. 18. Burreed formed an important part of the redhead nesting and juvenile rearing cover. (Photo by Ada Hayden.)



FIG. 19. Good duck nesting cover destroyed, 1939. The farmer seldom gains from such practices.

of the plants was in approximately 12 inches of water.

5. Sedges-Spike rushes-Whitetop Community.—These minor plants grew in shallow water and were of very little importance in rearing cover. Seven (2.45 percent) broods were observed in this community.

6. Willow Community.—Since the willows grow normally on the bank or in very shallow water, they have little value as rearing cover for redhead ducklings. Prior to 1937, water levels in general had been low with the result that willows had invaded several of the shallow bays of the Growing Pond and Smith's Slough. In 1940 dead and dying willows helped serve as cover for ten broods (3.5 percent).

Many minor aquatic plants were used occasionally as cover but because of their scarcity were not important as juvenile rearing cover. More abundant of these were the softstem bulrush, arrowhead, false indigo (*Amorpha fruticosa*) and several species of sedge.

Changes in water depth affect the rearing cover plants in a number of ways, two of which are important to redhead juvenile rearing. Either the cover is rendered useless by the water receding from the plants, or over a period greatly increased water depth may bring about a drastic reduction in the amount of cover. Measurements taken during the three-year study indicate that the water level increased in the lakes nearly 15 inches during 1938, and from watermarks on the banks and vegetation a similar increase took place in 1937. In early spring the ice shifting from one side to the other in the Growing Pond apparently was one of the factors which reduced the amount of cattails by up-rooting the plants. Little ice shifting was observed in shallow water.

Another factor important in evaluating the use of cover plants was the degree to which muskrats used a plant for lodge construction. Lodges and matted vegetation were used extensively by redhead broods on which to rest and sleep. Cattails, reed grass and burreed were utilized more heavily than the other plants by muskrats and were likewise most heavily utilized by redhead broods.

JUVENILES ON THE WATER

Since redhead ducklings were hatched in or near the rearing area in a nest normally surrounded by water they experienced little difficulty in reaching the rearing grounds. The length of time which the juveniles remained in the nests after hatching varied from three hours in some nests to 18 hours in others. The time of day when the juveniles left the nest depended largely upon the time of hatching, the disturbance at the nest and probably the degree of exposure of the nest, though little direct evidence was found for the latter. Data on four nests showed that the juveniles were led from the nest shortly after the ducklings were dry, while in two other nests juveniles which hatched in late afternoon were still in the nest the following morning.

Because of the mobility of the juveniles the area

over which they traveled was limited only by the size of the rearing habitat. In an effort to determine movements, colored feathers were glued to the top of the heads of 48 juveniles. Although not entirely satisfactory as a method of marking ducklings, the feathers did indicate movements of some of the juveniles. One week after banding nine juveniles on the nest in the southern end of Barringer's Slough the brood was observed in the Growing Pond, two miles from their nest. Broods often traversed the 40-acre Growing Pond several times daily, these aggregating a total distance of half mile or more.



FIG. 20. Outlet of Lost Island Lake, August, 1935. Bulrushes, cattails, smartweeds, and duck potatoes furnished nesting and rearing cover and food for ducks.

Juveniles seldom were observed on dry land. Muskrat lodges, muskrat feeding platforms, floating logs, boards, old coot nests, and plant debris were used as resting and sleeping places.

The feeding routine of the ducklings, irregular at first, became more regular as they grew older. At dawn the partly-grown juveniles climbed from the night roosts on muskrat lodges and fed intermittently for two to three hours, after which they rested in the dense cover until late afternoon. Another period of two to three hours before dark was spent alternately feeding and resting. Juveniles during the first four to five weeks followed the female closely as she led them to choice feeding sites. The juveniles at times darted away in quest of insects and food, but were recalled frequently by the female. Close compact formations were assumed when the ducklings were frightened and when they traveled from place to place.

Because of the difficulties in capturing juveniles, growth rate information was secured in only a few instances. The data taken showed that the largest juvenile captured weighed 951 grams at approximately 11 weeks of age. Juveniles one to two days old weighed about 50 grams.

Juveniles at eight weeks of age flapped over the water and flew at 10-12 weeks of age. They practiced flying during the mornings and evenings while feeding and chasing one another. The longest juvenile flight observed lasted eight minutes during which the juvenile flew back and forth across Round Lake



FIG. 21. Outlet of Lost Island Lake, summer of 1940. Duck nesting and rearing cover gone. Water had increased 24 to 30 inches in depth.

(450 acres) as if testing his newly developed skill. The first flight of the juveniles was observed August 20, although the first juveniles of the year probably flew as early as August 10. Often fully grown juveniles capable of flying were captured when they chose to dive into the vegetation-choked water rather than take to their wings.

Limited intermixing of broods undoubtedly took place during the first six weeks of life but the number of juveniles to a brood remained very nearly the same. Broods above six weeks of age had a tendency to band together. A concentration of juveniles estimated to be above eight weeks old was noted in the Growing Pond and was coincident with the apparent desertion of the broods by females. However, it was not entirely clear whether a female deserted a brood or vice versa, since females were often observed with only one or two juveniles from their broods, the rest of which were taking care of themselves. By August 24, when the average age of broods was 10 weeks, only seven percent of the broods counted had females in attendance (Table 19).

TABLE 19. Summary of redhead brood data.

Date	Number of broods	Number young per brood	Broods with females, in percent	Approximate brood ages, in weeks
June 1-7.....	1	9.0	100	0.6
June 8-15.....	1	9.0	100	0.3
June 16-23.....	4	6.2	100	1.0
June 24-30.....	3	8.0	100	1.5
July 1-7.....	10	7.6	100	1.5
July 8-15.....	40	7.0	90	2.0
July 16-23.....	41	6.2	97	3.0
July 24-31.....	59	7.2	96	4.0
Aug. 1-7.....	77	7.0	95	6.0
Aug. 8-15.....	33	6.5	78	7.0
Aug. 16-23.....	14	6.2	43	9.0
Aug. 24-31.....	29	6.5	7	10.0
Sept. 1-7.....	10	5.3	..	12.0
Total and average.....	322	6.8

BROOD COUNTS AND JUVENILE MORTALITY

As a means of evaluating numerically the productiveness of the species and of determining the amount of juvenile mortality, brood counts were made each year from June 1 until the promiscuous flocking habits of the ducklings, which usually preceded the dispersal and disappearance of the broods, rendered the counts unreliable.

A total of 322 broods were counted: 80 in 1938, 180 in 1939, and 62 in 1940. Tri-weekly counts of broods were made on all water areas under observation in addition to recording broods observed at other times during the investigation. Observations were made while tramping or boating through marshes and sloughs and from such vantage points as roads, trees and windmills near juvenile rearing areas. On the small potholes and marshes best results were obtained by wading the margins of the areas which caused many of the broods to move from the protection of the vegetation near the shores to open water where counts were made with the aid of field glasses. The partly open Growing Pond presented a unique opportunity to observe broods at close range, and there 78 percent of the broods were recorded. Ten percent were on Barringer's Slough.

Broods were more easily seen early in morning and late in afternoon during the feeding periods. The time of observation was recorded for 260 broods of juveniles. One hundred and twenty-two broods (46 percent) were recorded between 5:00 a.m. and 8:00 a.m., 78 broods (28 percent) between 8:00 a.m. and 3:00 p.m., and 60 broods (26 percent) between 3:00 p.m. and 7:00 p.m.

As shown in Table 20 the normal distribution of broods fell between 1 and 15 juveniles with most broods between 4 and 9 individuals. Means for July and August were 6.9 and 6.7 juveniles to a brood. June and September brood counts, although not too reliable because of the small numbers of broods counted and the disposal of the broods in the latter

TABLE 20. Frequency of occurrence of redhead brood sizes, 1938-1940.

Size Class	June	July	August	September
1.....	..	1	..	1
2.....	2	2
3.....	..	14	11	..
4.....	1	9	26	1
5.....	..	12	19	3
6.....	3	30	24	1
7.....	1	21	10	..
8.....	..	19	29	..
9.....	3	30	17	..
10.....	..	5	11	1
11.....	1	1	3	..
12.....	..	3	4	..
13.....	..	2	2	1
14.....	..	1	1	..
15.....	..	1
Totals.....	9	149	153	10
Average size brood...	7.4	6.9	6.7	5.6

month, indicated a trend from larger broods in June to smaller broods in September. The small broods of September were juveniles presumably from late renests and partial broods of older juveniles. Earlier, in Iowa, an average of three juveniles in nine broods of redheads with a minimum of one in the smallest brood and a maximum of five in the largest brood was recorded (Travis 1939). In Canada an average of six juveniles in six broods was observed during July (Furniss 1938), and in Minnesota 5.5 young for 14 broods were reported (Smith 1941).

Brood counts showed that after the ducklings became seven to eight weeks of age the female no longer attended them. There was no large concentration of juveniles as they attained maturity, but rather the older juveniles of flying age gradually disappeared from the research area. By September the juveniles were scarce, and none was recorded after October 10.

Broods tallied according to their approximate ages showed that the greatest period of mortality was during the first few days of life. An average of 6.9 juveniles was recorded in 40 broods less than a week old. The average successful clutch hatched out 9.1 juveniles. This indicated a loss of approximately two juveniles to a brood during the first week after hatching. However, the loss was not large after the first few days of life for the average brood contained 6.9 juveniles near the end of the first week and 6.3 juveniles at the end of six weeks, a decrease of 30 percent from the average successful clutch at hatching. About seven weeks of age the broods began banding together and after attaining the age of flight the groups became smaller as the birds left the research area.

TABLE 21. Size and age of broods.

Age in weeks	Number of broods	Size of broods
0-1.....	40	6.9
1-2.....	77	6.7
3-4.....	71	6.5
5-6.....	58	6.3
7-8.....	30	7.5
9-10.....	20	7.7
11-12.....	26	6.6

Known causes of juvenile mortality were comparatively few. Security offered by the water and vegetation in which ducklings remained during the rearing period rendered them comparatively safe from terrestrial predators. Evidence of predation was difficult to detect because of the sparse population and because the large amount of rearing cover available could easily have hidden carcasses and other mortality evidence. Mink were common on all the marshes, but examination of seats gathered along the shores did not reveal evidence of juvenile redheads. Coot juveniles were present in nearly all mink seats collected by the writer during June and July. Bennett (1938a) was of the opinion that the abundant and unwary coot chicks acted as a buffer for blue-winged

teal ducklings, and the same may have held true for redhead juveniles. One two-week-old juvenile partly devoured, presumably by mink, was found in 1940. Another dead juvenile with one leg torn off was found in the open water of the Growing Pond.

TABLE 22. Time of beginning of clutches for successful nests and for redhead broods, 1938-1940.

Period in which clutches began	Successful nests under observation	Total broods observed in the field relegated to periods in which nests were begun			
		1938	1939	1940	Totals
May 1-10.....	17	3	9	15	27
May 11-20.....	30	7	10	13	30
May 21-31.....	19	12	14	7	33
June 1-10.....	13	7	5	4	16
June 11-20.....	5	2	2	2	6
June 21-30.....	1	1	..	1	2
July 1-10.....	2
Totals.....	87	32	40	42	114

Three other causes of juvenile mortality were noted. Three juveniles were found dead on as many nests where they were crushed by the females at the time of hatching, and five juveniles died of exposure when they hatched after the females had left the nests with the first hatched ducklings. One clubfoot duckling, unable to move, was found in a renesting attempt.

Evidence of lead poisoning in juveniles was restricted to one nearly full-grown duckling, while four adults were found dead from lead poisoning during the same period. An examination of 25 square-foot soil samples taken from the bottoms of five of the marshes showed that 64 percent of the samples contained an average of two shot. In these samples there were about 518 times as many small gravel pebbles, 25 times as many small snail shells and 60 times as many seeds of aquatic plants as lead shot. The abundance of gravel, shells, and seeds rendered unlikely any large amount of lead poisoning in the research area.

Leeches (*Theromyzon occidentalis*) were found parasitizing juvenile and adult redheads. The small greyish-white leeches not more than one-quarter inch long were observed making their way into the eye and nasal cavities of the ducks captured for banding. As many as six dark colored leeches one-half inch long and one-quarter inch thick were taken from the nasal cavities of some juveniles. Captured juveniles expelled smaller leeches by "sneezing." Eighty percent of the 4 to 11 week old young were hosts to leeches, but juveniles above the age appeared free of the parasites (Table 23). Two adults found dead from lead poisoning were heavily parasitized by leeches. No mortality was found directly attributable to leech parasitism.

Ecto- and endo-parasites of the redheads observed in this investigation were identified by the United States Fish and Wildlife Service. A flatworm (*Diploposthe* probably *laevis*) was taken from the intestine of one juvenile bird, while a fluke (*Echino-*

TABLE 23. Leeches parasitizing juvenile redheads, Ruthven, Iowa, 1940.

Approximate age of ducklings in weeks	Numbers of ducklings examined	Average number of leeches present
1 day.....	40	0
3-4.....	1	3
4-5.....	5	1.2
6-7.....	2	2.5
9-10.....	5	3.3
11-12.....	2	0

stoma revolutum) was found in an adult bird. Tape-worms (*Hymenolepis* spp.) were common in both juvenile and adult birds. Lice from young and old birds included *Trinoton querquedulae*, *Anetoecus dentatus* and probably *Menopon loomisii*.

FALL MIGRATION

Signs of fall migration became evident as early as August 20. By that date many of the juveniles were flying and their unrest together with flights which daily grew longer indicated that migration from the area was imminent.

As the juveniles approached two months of age they became difficult to distinguish in size from the females. The number of broods observed with females lessened until during the week September 7-15 only two broods with females were observed. The juveniles left shortly after they were able to fly. Redheads, individually or in two's and three's observed late in September on large open lakes as Round, Virgin, and Trumbull lakes and smaller open bodies of water indicated they were spreading from their rearing grounds in all directions as though testing their wings on short flights before leaving for an unknown destination. Some light is shed on the dispersal of juveniles by returns from North Dakota of three bands taken from young birds killed in the first fall after they were banded in the Ruthven area. The flight of the juveniles from the research area preceded the main redhead flight from the north by nearly a month.

The number of fall migrants in the area at one time was approximately one-half to two-thirds the number of spring migrants. Only the lakes and marshes with food and protection were resorted to by the redheads in fall migration. Before the hunting season opened October 22, 1939, fall migrant ducks were present on many lakes and marshes. With the beginning of the hunt ducks soon left small lakes and marshes and concentrated in refuges and on large open lakes where safety was assured. The peak of the fall migration was reached about October 23-30, and by November 5, most of the redheads had left the Ruthven area, long before the lakes froze over or the food supply was exhausted.

Spirit and Okoboji lakes, larger than the lakes of the research area, in Emmett County, were used by much larger numbers of fall migrant redheads than those of the Ruthven area.

HUNTING

In 1939, 293 hunters were interviewed in the field to ascertain the success of the hunt and to obtain their opinions of the hunting conditions. All species of waterfowl were included in the data (Table 24). Data were obtained on: (1) marsh shooting in which block decoys were used by the majority of veteran hunters, (2) pass shooting in which hunting was done on the natural narrow flyways used by waterfowl in passing from one lake to another, and (3) shore walking and jump shooting. Often hunters were unwilling to recall the numbers of cripples lost, while other were willing only to report the numbers and kinds of birds obtained. Veteran hunters as well as amateurs had difficulty in judging crippling. Reported crippling losses varied from no cripples to 100 percent, with an average of 25 percent loss.

Redheads constituted approximately five percent of the bagged birds checked during the 1939 season. Very few legal limits of redheads were taken. Those hunters who shot over natural flyways between lakes secured the majority of redheads shot, while those hunters in the large marshes shot the next highest numbers. Only an occasional redhead was shot by shore walkers and jump shooters. Thirty-seven percent of the ducks bagged were mallards, 16 percent were green-winged teal, and 13 percent lesser scaup.

The 293 hunters interviewed in 1939 shot an average of 4.7 birds per hunter day of which 3.5 birds were bagged. The loss of 1.2 birds a day (25 percent) is considered a very conservative estimate of the hunters' loss.

TABLE 24. Duck hunting loss, Ruthven Area, 1939.

Type of shooting	Class of shooter	Number of hunters	Birds shot	Birds bagged	Birds lost	Percent of loss
Marsh (including decoys)...	Veteran	105	642	508	134	21
	Other	52	280	187	93	33
Pass shooting...	Veteran	52	208	166	42	20
	Other	67	189	124	65	34
Shore-walking and jump-shooting.....	Veteran	2	13	12	1	8
	Other	15	64	47	17	26
Subtotals.....	Veteran	159	863	686	177	20
	Other	134	533	358	175	33
Totals.....		293	1396	1044	352	25

In 1932, 1,315 ducks were shot by 106 hunters during the duck hunting season with a 50 percent crippling loss, and the greatest loss was in pass shooting by non-veteran hunters (Errington & Bennett 1933).

A survey of the duck hunting grounds within the research area, exclusive of corn fields, showed that the state owned and controlled approximately 5,000 acres of public shooting grounds for waterfowl and that about 1,500 acres of available hunting grounds were privately owned. Of the 5,000 acres of state-owned waters about 600 acres (11 percent) were considered good for hunting, while 1,400 acres (93 percent) of the privately owned lands were considered good. Approximately 94 percent of the private

land was owned or leased by hunting clubs and sportsmen's organizations whose membership in 1939 totaled about 100.

During the first day of hunting in 1939 an estimated 1,200 hunters were at the research area, one-half to two-thirds of whom were pass shooting and the remainder marsh shooting. Such a concentration represented about one hunter to an acre of marsh on public shooting grounds and concentrations upwards of 50 shooters to 100 yards in favored pass shooting areas. On private lands during the first day of the season one hunter was present to 18 acres. A summary of the hunting territory exclusive of cornfields in the Ruthven area is given in Table 25. The usual daily numbers of hunters on both private and public lands decreased as much as 75 percent after the first day or two.

TABLE 25. Summary of hunting territory, Ruthven Area, 1939.

Owner-ship	Acres large open water lakes	Acres dry areas	Acres good shooting areas	Acres refuges	Miles good pass shooting	Acres private gun clubs	Acres open to public
State . . .	3540	572	600	450	3	1425	4712
Private . .	100	100	1405	...	1.25	1425	80
Totals . . .	3540	672	2005	450	4.25	1425	4792

The greatest need of refuges and sanctuaries for the redheads in Iowa is during the shooting season. Although not designated as such the open lakes of the research area served well the protective function of refuges for the redheads and other diving ducks. Round Lake, the one posted refuge of the Ruthven area, and Trumbull, Elk, Virgin and Lost Island lakes appeared adequate for protection of the red-

heads during the hunting season and as resting and feeding sites during the spring.

YEARLY PRODUCTIVITY

That the productivity of a given game bird in the wild is often not equivalent to the success of the nests which the investigator has under observation is becoming increasingly clear (Errington 1942).

It was known from the redhead nests under observation that 56.2 percent produced an average of 9.1 juveniles each. Thus, for every 100 nests 511 juveniles were hatched from normal clutch-size nests and 45 juveniles from the known renesting attempts, a total of 556 juveniles. Since, however, only about 70 percent of the juveniles reached maturity, a total of 398 juveniles reached the migratory stage for each 100 nests.

In an attempt to determine the productivity of the redhead population in the Ruthven area as based on the percentage of successful females analysis had followed that presented by Errington (1942). From nests actually under observation 56 percent hatched which does not, however, represent the true percentage of successful females. It was known that all re-nesting attempts did not come at the end of the season but that new nests were built to replace some of the earlier unsuccessful ones. Thus, early nest failures did not necessarily mean failure of the female to bring off a brood of young.

In attempting to arrive at a figure representing the percentage of successful females two difficulties were encountered in the analysis: (a) the interval which elapsed from the time a nest was destroyed until a new clutch was started was not definitely known, and (b) the dates on which nests were begun were not definitely known but were calculated from the time of hatching, the age of the brood or the num-

TABLE 26. Probable renesting attempts of redhead females after previous failures, Iowa, 1938-1940. Numbers in parentheses are percentages.

Period in which failed clutch was begun	Number of clutches failing	Number of failures terminating breeding efforts	Number of failed clutches for which renesting attempts might subsequently be made and the period of possible renesting						
			May 11-20	May 21-31	June 1-10	June 11-20	June 21-30	July 1-10	July 11-20
May 1-10 . . .	8 of 25	..	2 (25.0)	2 (25.0)	..	4 (50.0)
May 11-20 . . .	16 of 47	..	1 (6.2)	1 (6.2)	4 (25.0)	5 (31.2)	2 (6.2)	3 (18.7)	..
May 21-31 . . .	11 of 29	3 (30.0)	2 (20.0)	3 (30.0)	2 (20.0)
June 1-10 . . .	13 of 24	6 (50.0)	1 (12.5)	3 (25.0)	1 (12.5)	1 (12.5)
June 11-20 . . .	4 of 9	1 (25.0)	2 (50.0)	1 (25.0)
June 21-30 . . .	1 of 2	1 (100.0)
July 1-10 . . .	4 of 6	3 (75.0)	1 (25.0)

ber of eggs in incomplete clutches. Because of these difficulties the figures for the number of females producing young cannot be too accurate but it is believed is much nearer the correct figure than has been presented before.

Broods of young redheads were counted during the entire seasons of 1938-1940. Females remained with the broods until the juveniles were about six weeks old (Table 19) although few broods of all ages were noted without females. In order that the data be as accurate as possible only those broods with females were included for analysis. Again, brood data were discarded on broods which were known to have been observed more than one time.

Calculations on the probable dates of renesting (Table 26) were based on the relative advancement of the unsuccessful clutches at the time of failure. Periods between peaks of nest failure and subsequent peaks of nest building were in the second 10-day period following nest failure (Fig. 9). Females which had not completed a clutch at the time of nest failure normally could be expected to start laying earlier than females which had started incubation at that time. Thus, females with few eggs or incomplete clutches were calculated to resume laying during the following 10-day period after failure, while females with partially incubated clutches were calculated to resume laying during the second 10-day period following nest failure.

The total number of females during the three-year period involved in nesting activities up to June 10 was 154. The distribution by 10-day periods was as follows: May 1-10, 40 females; May 11-20, 44 females; May 21-31, 46 females; June 1-10, 22 females. All nests commenced after June 10 were undoubtedly renestings as judged from the small numbers of eggs and poor nest construction and it was then assumed that all initial nestings were completed.

Calculating the data on a sample of 100 redhead females it was found that approximately 80 percent of the females produced young during a typical season and that from these 100 females slightly over 600 young were produced, approximately 6 young to a nesting female or about 8 young to each successful female (Table 27).

TABLE 27. Calculated productivity of a sample of 100 redhead females, Ruthven, Iowa, 1938-1940; based on data in Tables 7, 10, 22.

Period during which clutches were begun	Calculated number of females laying in initial and renesting attempts	Calculated number of clutches successful	Calculated number of hatched young
May 1-10	25.8	18.2	149
May 11-20	32.6	20.2	172
May 21-31	32.9	21.5	170
June 1-10	20.2	10.9	94
June 11-20	8.9	4.9	34
June 21-30	3.9	1.9	17
July 1-10	9.1	3	15
Totals	133.4	80.6	651

FOOD HABITS

Because of the relative fewness of redheads on the research area no juveniles or adults were collected for laboratory food habits work. Four gizzards were taken during the fall hunting season of 1939 from redheads shot by hunters and three from birds found dead. The gizzards of the ducks found dead, however, were empty. Martin & Uhler (1939) have presented the status of wild duck foods in the United States in general, while Kubiehek (1933) and Cottam (1939) have recently reported on detailed studies of the food habits of the redheads.

The following brief summary of food habits of the redhead has been taken from Cottam's "Food Habits of North American Diving Ducks" (1939). Although some of the food items of the redhead in the Ruthven area may be slightly different because of availability of different food plants the general food habits are undoubtedly the same. From a total of 364 gizzards from adult ducks reported upon by Cottam the food was found to consist of 89.66 percent plant and 10.34 percent animal food. Pondweeds (*Najadaceae*), the most important group of plants eaten, formed 32.27 percent of the food of the redheads. One or more species of *Potamogeton* were present in over half of the gizzards examined. Sago pondweed composed 9.06 percent of the food while other pondweeds furnished 15.54 percent of the food. Wigeon grass (*Ruppia maritima*) and naiads (*Najas flexilis*, *N. guadalupensis*, and *N. marina*) formed 6.62 percent of all foods consumed. Musk grass (*Chara* spp.) and algae contributed 7.72 percent of the food. Grasses, largely from wild rice (*Zizania aquatica*), whitetop (*Fluminea festucacea*) and *Panicum* composed 6.25 percent of food. Other foods in smaller amounts were wild celery (*Vallisneria spiralis*), duck weeds (*Lemna* spp.), waterlilies (*Castalia* and *Nymphaea*), coontail (*Ceratophyllum demersum*), smartweeds (*Polygonum* spp.) and other miscellaneous aquatic plant seeds and plant foliage.

The 10 percent of animal food taken was over half insects (5.89 percent) of which grasshoppers (*Orthoptera*), midges (*Chironomidae*) and caddisfly (*Trichoptera*) were in approximately equal proportions. Mollusks, principally gastropods, constituted 3.86 percent of the food, mostly during winter months along the coasts.

In the present study the use of plants as food was noted, and whenever possible a check was made of the vegetation in the immediate vicinity of feeding redheads as a supplement to stomach analysis studies. Most abundant of the aquatic food plants in the lakes and marshes of the Ruthven area were the sago pondweed, longleaf pondweed (*Potamogeton americanus*), bladderwort (*Utricularia vulgaris*), duckweeds, dotted wolffia (*Wolffia punctata*), awned sedge, lake sedge, hardstem bulrush, and several species of smartweed. Small isolated stands of wild rice and wild celery were present in the research area but were considered relatively unimportant as foods because of their scarcity. Musk grasses were present in abundance

TABLE 28. List of the more abundant aquatic food plants in the Ruthven Area, Iowa, 1938-1940. Relative abundance: A, abundant in all shallow-water areas under observation; B, found scattered in most of areas; C, occasional plants or communities; D, scarce (widely scattered) or in localized areas only. Parts available: L, leaves; R, roots; S, seeds; ST, stalks; T, tubers; WP, whole plants (including seeds).

Name of Plant	Relative Abundance	Parts Available
Submergent Vegetation:		
Slender naiad (<i>Najas flexilis</i>)	B	WP
Guadalupe naiad (<i>Najas guadalupensis</i>)	D	WP
Long-leaved pondweed (<i>Potamogeton americanus</i>)	C	S
Leafy pondweed (<i>Potamogeton foliosus</i>)	C	WP
Grass-leaved pondweed (<i>Potamogeton gramineus</i>)	C	WP
Sago pondweed (<i>Potamogeton pectinatus</i>)	A	WP
Clasping-leaved pondweed (<i>Potamogeton Richardsonii</i>)	C	WP
Flat-stemmed pondweed (<i>Potamogeton zosteriformis</i>)	D	SLR
Coontail (<i>Ceratophyllum demersum</i>)	A	WP
White water crowfoot (<i>Ranunculus trichophyllus</i>)	D	S, L
Yellow water crowfoot (<i>Ranunculus flabellaris</i>)	D	S, L
Water milfoil (<i>Myriophyllum spicatum</i>)	C	S, L, ST
Musk grass (<i>Chara</i> spp.)	A	WP
Greater bladderwort (<i>Utricularia vulgaris</i>)	A	WP
Fresh water eel grass (<i>Vallisneria spiralis</i>)	D	WP
Floating Plants:		
Lesser duckweed (<i>Lemna minor</i>)	B	WP
Star duckweed (<i>Lemna trisulca</i>)	B	WP
Greater duckweed (<i>Spirodela polyrrhiza</i>)	A	WP
Dotted wolffia (<i>Wolffia punctata</i>)	B	WP
Emergent and Shore Vegetation:		
Burreed (<i>Sparganium eurycarpum</i>)	A	S
Lophocarpus (<i>Lophocarpus calycinus</i>)	C	S
Arrow-leaved arrowhead (<i>Sagittaria cuneata</i>)	B	S, T
Broad-leaved arrowhead (<i>Sagittaria latifolia</i>)	C	S, T
Whitetop (<i>Fluminea festuacea</i>)	B	S
Meadow grass (<i>Glyceria striata</i>)	D	S
Prairie cord grass (<i>Spartina pectinata</i>)	C	S
Wild rice (<i>Zizania aquatica</i>)	D	S
Awed sedge (<i>Carex atherodes</i>)	A	S
Lake sedge (<i>Carex lacustris</i>)	A	S
Beaked sedge (<i>Carex rostrata</i>)	B	S
Water sedge (<i>Carex aquatilis</i>)	B	S
Diffuse tussock sedge (<i>Carex stricta</i> var. <i>strictior</i>)	C	S
Chufa (<i>Cyperus esculentus</i>)	D	S, T
Shining cyperus (<i>Cyperus rivularis</i>)	D	S
Hardstem bulrush (<i>Scirpus acutus</i>)	A	S
River bulrush (<i>Scirpus fluviatilis</i>)	A	S
Slender bulrush (<i>Scirpus heterochaetus</i>)	C	S
Softstem bulrush (<i>Scirpus validus</i>)	C	S
Baltic rush (<i>Juncus balticus</i>)	C	S
Marsh smartweed (<i>Polygonum coccineum</i>)	B	S
Nodding smartweed (<i>Polygonum lapathifolium</i>)	C	S
Blunt-leaved water smartweed (<i>Polygonum natans</i>)	C	S
Largeseed smartweed (<i>Polygonum pennsylvanicum</i>)	C	S

in some of the shallower lakes and marshes, and algae, particularly of the genus *Pithophora* and *Rhizoclonium*, formed blankets of considerable size on some lakes.

The feeding habits differed as the season advanced

from spring to fall. Ice covered the normal feeding habitats of diving ducks in 1940 until March 29, a week after the first flight of redheads was sighted. The absence of redheads during the week following the first flight in 1940 may possibly be correlated with the inaccessibility of food. Early migrants fed in large flocks, but as the nesting season approached the ducks were often observed feeding in pairs or singly. Coots, baldpates and blue-winged teals were often observed feeding on the vegetation brought to the surface of water by redheads and other diving ducks. At times, however, other ducks and coots were chased away by the male or female of a pair of redheads.

Periods of most active feeding for adults were in early morning from dawn until about 8:00 or 9:00 a.m. and again in the evening for two or three hours. During cold periods, however, the ducks fed at intervals throughout the day. Incubating females also fed at intervals throughout the day. The ducks were observed feeding after dark on moonlit nights and feeding was noticeably sporadic during mornings following moonlit nights.

The duration of any one feeding period lasted from a few minutes to two hours, the longer periods being noted during migration. Adults and nearly full grown juveniles diving in four feet of water remained under the water an average of 11 seconds, between the extremes of five and 15 seconds. The interval between successive dives varied from a few seconds to several minutes.

The first week to ten days after hatching juveniles remained very close to a female. Diet of the first week or two was gathered from the surface of the water. With quick eager rushes the ducklings, necks outstretched, grabbed at surface insects. From two to four weeks of age the juveniles divided their time between feeding on the surface of the water gathering flies, small moths, mayflies and other insect life above the water and part time feeding with the bill beneath the surface of the water often in dense growths of duckweeds and dotted wolffia. At four to five weeks of age juveniles commenced diving for food and at six weeks of age many juveniles were observed feeding in four to six feet of water. Since most of the aquatic food and cover plants grew in 12 to 18 inches of water it was in this depth of water that juveniles were most frequently seen feeding.

Excellent food plants were abundant enough in all the marshes that food was not considered a limiting factor in the selection of nest sites or rearing areas. A list of the more abundant aquatic food plants occurring in the Ruthven area is given in Table 28. Additional details and a list of the plants of the Iowa lake region has been published by Hayden (1943).

MANAGEMENT PRACTICES IN RELATION TO THE REDHEAD

The welfare of the redheads as well as other waterfowl is affected by a number of conditions, some of which have been recognized for some time while

others have only come to light within the past few years. In general, three major and numerous minor factors have been working against the biological productivity of the redheads and until recent years pulling the population ever lower. Three major factors, two of which are directly man-made and which probably influence the effects of the third, are (a) overshooting, (b) drainage of nesting habitats, and (c) drought. Among the many minor causes of duck mortality which occasionally reach undue severity in scattered localities are botulism, lead poisoning, parasites, and diseases.

Since the breeding territory of the redheads which lies practically entirely within the agricultural belt of the United States and the Prairie Provinces of Canada was largely destroyed by the recent drought period, 1934-1938, this species has been more seriously affected than other members of the diving duck group. Again, successive encroachment through reclamation and agricultural operations within the agricultural belt has deprived the redheads of many of the choicest nesting grounds. Moreover, the peculiar nesting requirements of the redheads, shared largely with the Ruddy Duck, limit the amount of nesting cover available during any one season. Optimum productivity of redheads can be most effectively assured through the fulfillment of the habitat requirements of the bird. All of the requirements and interrelated factors necessary to the best welfare of the bird are not by any means known, but certain of the required conditions are known. Since no panacea exists which will produce an abundance of these birds without suitable environmental conditions, the recognition of these environmental needs of the redhead must precede the efficient management of water areas favorable to this waterfowl species. The presence of the two environmental conditions, (a) water a few inches to a foot or more deep, and (b) suitable emergent vegetation within the habitat, are essential to the successful production of redheads in Iowa marshes and lakes. A discussion of these two essential needs must consider certain phases of the nesting, the juvenile rearing, and the spring and fall migrations. The following discussion which undoubtedly has applicable points elsewhere in the breeding range of the redheads has as its focal center the glacial lake region of north-western Iowa.

ENVIRONMENTAL CONDITIONS

WATER REQUIREMENTS

Management plans and practices designed to produce more desirable nesting habitat for redheads must deal with water conservation. Practically the entire lives of redheads except during flight is spent on water. Water directly or indirectly determines the aquatic vegetation which the birds use as nesting cover. Thus, acquisition, maintenance, and manipulation of water and of water levels are the keys to more favorable environmental conditions for redheads.

Although the large lakes (500-1,000-up acres) did not provide ideal nesting territory, they were chosen

by the ducks during the spring migration as resting, feeding, and courtship areas. The ducks did not appear to be attracted during migrations to the actual nesting habitats and cover, but rather to the large lakes and marshes. Many sloughs and marshes that had ideal conditions for nesting were not frequented by the redheads until a nesting site was desired. At this time the ducks left the larger lakes for the nearby marsh habitats.

Practically all of the lakes within the Ruthven area were frequented by redheads during the spring flight, but the ducks remained only on those lakes or marshes where nesting cover could be found within a short distance. Elk and Virgin lakes, and Greene's Slough were attractive to migrant redheads but not to nesting redheads. Mud, Round, Trumbull, and Lost Island lakes, each of which had good nesting cover nearby, were frequented by the ducks during the migration as well as during the nesting seasons.

The redhead nests were often grouped in the nesting cover, while other parts of the nesting cover within the same marshes or nearby water area equally suitable to nesting as far as could be determined were often not utilized. Where one nest was located others were usually found nearby. Particularly was this tendency to nest close together true in parts of Barringer's Slough, Mud Lake and certain of the potholes of Dewey's Pasture. A concentration phenomenon was observed in the courtship and mating of the ducks. Prior to nesting certain areas were chosen by the ducks upon which they carried on courting activities. Females were observed coming to these chosen areas during the middle of the day from different parts of the marshes, presumably from their nests or nesting sites. Whether this tendency to group nests together indicates a psychological or physiological function desirable for nesting or is connected in some way with courtship and mating activities which are often performed by groups of the birds is not clear. However, there appears to be some unknown element in addition to the favorable environmental qualities in the nesting cover which influences the choice of the nesting sites.

From the sporadic grouping of the nests within the habitats and the apparent tolerance of the nesting redheads for other nesting waterfowl, it appeared that the existing nesting cover was not fully utilized by the comparatively few redheads which spent the summer in Iowa. Whether or not the total numbers of ducks which stop to nest on the southern periphery of their normal breeding range can be materially increased is open to question. However, nesting habitats can be made more productive of redheads and thus help build up a local breeding population by eliminating some of the more destructive factors operative on the ducks which do nest in the Iowa marshes.

AREA OF WATER HABITAT DESIRABLE FOR NESTING

Regardless of the apparent tendency of the redheads to nest in groups, certain environmental conditions determined the relative success or failure of the spe-

cies to reproduce in a given habitat. The water habitat desirable for nesting was not conditioned by area alone but by its nearness to the large permanent bodies of water. Marshes of 10 to 20 acres or larger within a quarter mile of large permanent lakes were most heavily utilized by nesting redheads. From available data it appears that for nesting redheads a marsh or slough about five acres in area not further than one-fourth mile from a large lake is near the optimum. The small kettlehole ponds of Dewey's Pasture, easily accessible to the ducks from Mud Lake, represented the most favorable of the smaller redhead nesting habitats of the research area, while Barringer's Slough, used by the redheads as nesting and rearing cover, was characteristic of the larger nesting habitats.

MANIPULATION OF THE WATER LEVEL

Within the nesting habitats an adequate and at least partially controlled water supply is of prime importance to the nesting redheads. On the marshes which accommodated them the water level prevailing during the nesting seasons determined to a great extent the following: (a) the presence or absence of nesting, (b) the success or failure of the nests, (c) the selection of the cover plants used for nesting, and (d) the amount of nesting cover. A discussion of the foregoing conditions given under "Nesting" and "Nesting Cover" showed that the water level was a more important criterion in the selection of a nesting cover than a preference by the ducks for any of the more intensely used single plant cover species. When the water level rose rapidly nests already established were often flooded, and when the water level receded from around the nests they were deserted. Yearly variations in the numbers of nests evident in certain sloughs were attributed to a change in the water levels. The numbers of redhead nests on Smith's Slough and Mud Lake, which decreased over 90 percent in 1940 as compared to 1938 and 1939, correlated with a drop in the water level in 1940 which left over two-thirds of the nesting cover of the former area dry during the nesting season. The effect of water levels on the existing vegetation and on the development of the vegetation, to be considered later, is another important point in management of redhead habitats.

What practices can be carried out to retain and at least partially stabilize during the nesting season the water so essential to these birds? Construction of small check dams at the outlets of the ponds, sloughs and marshes has been the most widely used and probably the most successful means of retaining water in the small water areas. Small earthen dams at the exits of ponds and kettleholes in Dewey's Pasture have rendered a definite service in retaining water within these small nesting areas. Low-cost earthen dams not only aid in maintaining favorable water level for the redheads during the nesting season, but help maintain water throughout the summer when it is needed by the young coots and grebes which have difficulty traveling from one pond to another. The

value of favorable water depths for muskrat propagation adds another incentive for retaining water throughout the year in the natural water basins.

Care must be taken, however, that too much water is not retained since emergent aquatic plants are killed by deep water. Most of the nesting cover of redheads and rearing cover of all the waterfowl in Iowa marshes flourish in water one to four feet deep. Carp (*Cyprinus carpio*) find conditions favorable for them in marshes and sloughs where water is deep enough to protect fish during the winter. Carp increased with an increase in depth of water in Dan Greene's Slough during the current study, while the emergent and submerged aquatic vegetation decreased and almost disappeared from the slough during the same period. One of the most injurious effects which rough fish, as carp, have on the small waterfowl habitats is that of roiling the water which shades out and smothers submerged and young emergent aquatic plants. Marshes or shallow lakes have not in general been successful in the optimum production of waterfowl and fish. Small areas with water deep enough for fish are often free of aquatic vegetation, and areas free of vegetation have little appeal to waterfowl. The maintenance of the water in small marshes and sloughs, which are primarily desirable as waterfowl habitats, to a level which will eliminate rough fishes is desirable.

Fluctuating water levels are not only harmful to the optimum production of marsh-nesting waterfowl and aquatic or semi-aquatic fur-bearing mammals, but are favorable to the development of excessive numbers of two of Iowa's most annoying mosquitoes, *Aedes vexans* and *Aedes trivittatus*. Life history observations on these mosquitoes reveal that the eggs are laid on the mud surrounding shallow temporary ponds and marshes in which the water is receding or drying up (Dyar 1928). Desiccation, followed by moisture, is favorable to the development and production of these mosquitoes. Thus, the role of a fluctuating water level in the life of these mosquitoes becomes apparent. Of the two mosquito control measures, (a) complete drainage and (b) stabilization or partial stabilization of water levels, the latter is preferable and could probably be more effectively executed. The problems of mosquitoes and waterfowl are of mutual interest on the larger marshes and sloughs particularly. Attainment and control of water levels in natural, restored, or artificial water areas cannot be overemphasized as favorable factors in the production of waterfowl and as a local measure in the prevention of excessively large broods of certain mosquitoes.

EMERGENT VEGETATION

Nesting Cover.—The second environmental element essential to a nesting habitat is emergent vegetation. Of the three most important cover plants, hardstem bulrush, lake sedge and narrow-leaved cattail, the ducks showed a slight preference for the bulrush. The choice of a plant species as nesting cover, however, was of secondary importance since the success

of the nest was dependent largely upon the water level. Nests located in bulrushes and narrow-leaved cattail were flooded less easily with a rise of water but with a recession in the water level were deserted just as readily as were the nests in sedges. Nearly equal distribution of nests within the area occupied by principal plant species does not suggest the need for particular encouragement of any one species, but suggests rather a control of water levels to bring about more successful nesting in the species that are chosen as nesting cover.

Interspersion of Cover.—In addition to a favorable water level the acceptability and use of plants by the redheads are governed largely by the interspersing of cover with open water. As previously discussed, a definite relationship existed between nearness of nests and open patches of water. Eighty-five percent of the nests were located within 50 yards of open water. This indicates that for optimum utilization of the vegetation there should be openings of at least a few square yards each in the nesting cover not farther apart than about one hundred yards. Cover in most marshes in the research area was interspersed by water in desirable amounts. However, the dearth of nests in several large blocks of dense cover which served as check areas showed the desirability of interspersed cover for nesting redheads.

Stands of emergent plants were broken up in the unmanaged marshes in three principal ways: (1) activity of muskrats, (2) elimination of certain plant species by fluctuation in the water levels, and (3) the dying out of plants from unknown causes in dense stands. Most emergent plants cannot stand excessive water depths nor can they stand excessive drought without dying or giving way to some other stage in plant succession. Over most of the unmanaged marsh land the fluctuation in the water level is one of the more important agents in interspersing dense nesting cover with open water areas. Large stands of cattail and reed grass were broken up during the study by an increase in water levels during a two-year period. At times very dense emergents died in spots in the interior of the stand which serves also to intersperse the cover. In the natural shallow basins found in most Iowa marshes the deeper water toward the center thinned or eliminated the vegetation. Controlled water levels appear to offer one of the most promising means of manipulating plant cover. Most of the water plants have a water depth preference and by manipulating the water depth these plants can be encouraged or discouraged.

Sixty-four percent of the nests were constructed in cover in which the nearest open water was around muskrat lodges. In addition to providing openings in the cover for nesting redheads, the lodges of muskrats created ideal waiting and resting places for both juveniles and adults. Old lodges grown up to weeds provided excellent refuge cover. One to three large muskrat lodges to an acre was sufficient to favorably intersperse the nesting cover.

In nesting habitats in which the cover is not inter-

persed by excessive fluctuation in the water level, muskrats or other natural agencies, various artificial methods may be employed. McAtee (1939) and Martin & Uhler (1939) have reported upon several phases in the technique of creating more favorable waterfowl habitat through the construction of ponds by blasting and digging or through the elimination of undesirable vegetation by the use of special mowing machines, saws and chemicals. Experimental work on blasting by the use of dynamite to improve the wildlife habitats on marsh land in Iowa by interspersing the dense cover and creating ponds has been reported upon by Scott & Dever (1940). Additional work with dynamite was carried out in the research area and in other localities in the state in an effort to obtain more evidence of the value of the clearings to nesting waterfowl. Improvement of marshlands for muskrats by ditching has added emphasis to interspersing of cover for wildlife.

An area in East Mud Lake, Palo Alto County, Iowa, was chosen in 1940 upon which to experiment. On these 120 acres of marshland the extremely dense vegetation was primarily lake sedge with scattered colonies of common cattail and water sedge. Water on the area was 15 to 18 inches deep in 1938 and 1939, although in the spring of 1940 only 4 to 6 inches of water were present. Insulation afforded by the dense vegetation prevented the ice from melting in the spring until May 15 or later. Eight clearings made in this habitat in April by the use of dynamite were approximately 36 to 48 inches deep, 8 to 12 feet wide and 75 to 125 feet long. The debris from the blasts was thrown 15 to 36 inches high around the edges of the clearings and provided resting and sunny sites for birds and muskrats. By varying the charges of dynamite in a particular spot an irregular edge was formed on the clearings. The water level receded from the area during 1940, leaving water only in the holes during the nesting season. Sufficient water was present, however, to be attractive to blue-winged teals and mallards, although not enough to be favorable for nesting of the redheads or ruddy ducks. In addition to the ducks which used the open water at the time of nesting, American bitterns, least bitterns, giant red-wings, yellow-headed blackbirds, numerous shore-birds, common mink, striped skunk, spotted skunk, and muskrat were observed on or around the openings. By the end of the first season after construction, arrowheads, duckweeds, and smartweeds were thriving in the water, while lesser ragweed, pigweeds (*Amaranthus* spp.) and other annuals were present on the banks of the clearings.

Several disadvantages were noted in carrying out this improvement work during the spring season. In addition to the ice which was present in the spring to retard the work, birds which were already on the area were frightened away. Other disadvantages which might be encountered in spring work are early spring rains which often raise the water level to such heights as to interfere with work. An abnormally high water level in a season might lead to the devel-

opment of an area with little or no water during the main nesting season. Habitat improvement work accomplished in the fall before the freeze-up would eliminate many of the disadvantages mentioned.

The construction of ponds as a means of interspersing cover by the use of trenching machinery or dynamite has the advantage over the use of mowers, burning or chemicals of being permanent for a number of years. Again, water left in these small ponds when the water levels decrease from protracted droughts renders the surrounding habitat attractive to puddle ducks.

AGRICULTURAL PRACTICES IN RELATION TO THE NESTING HABITAT

One of the two great causes, ranking with the disastrous drought of the early 1930's, in the reduction of redhead nesting habitat has been drainage of marshes and lakes for agricultural purposes. The dismal picture of the effects of drainage and drought at its worst on the nesting grounds within the United States has been admirably portrayed by Salyer (1934). Conditions were as bad in many parts of the Canadian prairie provinces. Although only a small part of the 100,000,000 acres of land drained in the United States and probably only a small fraction of the 6,000,000 acres of land drained in Iowa was formerly used by the redheads on which to carry out its life processes, many of the most fruitful redhead and other waterfowl breeding lands have been drained within the last quarter century. Little can be feasibly done to reclaim for duck production the marshes which today produce a good corn crop or other agricultural commodities. All of the marsh lands could not be successfully drained, however, and in Iowa approximately five percent of the marshland was unsuccessfully drained. In the interests of waterfowl perpetuation and increase the return to its original condition of every possible acre of unsuccessfully drained marsh land within the breeding range of the ducks should be the aim of conservationists. Paramount to the redheads is the restoration of those small prairie lakes, marshes and sloughs within the immediate vicinity of large open lakes or permanent marshes which first attract the ducks and on which the young are often reared.

Cutting of wild hay or marsh vegetation did not have a direct effect upon redhead production in the marshes of Iowa during the period of study, since haying was accomplished only when the water level was below that point favorable for redhead nesting. The practice of lowering the water level on marshes during the nesting season to facilitate haying may cause nesting failures. This practice should be curtailed where possible, at least until after July 1 when most of the ducklings are hatched. On the marshes of the research area lowering the water for haying was not practiced. Haying operations during a year when the water level is low may render the same area unsuitable for nesting redheads the following year even though the water level be favorable, because over 95 percent of nesting is carried out in

dead, dry cover of the previous season. Thus, even though haying operations may not directly affect the nesting, a reduction of nesting cover available for the ensuing year may result from such a practice.

The deleterious effect of excessive overgrazing and the advantage of moderate grazing on blue-winged teal nesting areas have been brought out (Bennett 1938a). With the exception of Dewey's Pasture, cattle were pastured on parts of the shores of all of the lakes and marshes utilized by redheads during the current study. No apparent ill effects to the nesting or nesting cover of the redheads resulted from livestock grazing. However, the damage that livestock can do to the vegetation of unprotected small ponds and marshes is well known, and all important duck habitats should be protected from excessive grazing. The depletion of the vegetation along shores and at inlets of marshes and sloughs resulting in soil erosion often cuts short the life of these water areas and their usefulness as habitats for the redheads. Many of the present open water lakes are becoming marshlands which in turn are becoming upland, a process hastened by the reduction and in many instances the depletion of the vegetation surrounding the natural water basins. Thus, in a state so intensively tilled as Iowa, water and soil conservation are of the utmost importance, and proper utilization of land surrounding marshes and lakes should be practiced. Only through the perpetuation and efficient management of the lakes and marshes can redheads be expected to survive and reproduce in Iowa.

REARING AREAS

Duck rearing cover plants in Iowa marshes were not a limiting factor in the production of redheads. Vegetation of the marshes used as rearing cover by juveniles was essentially the same species used for nesting cover. However, juveniles preferred deeper water toward the center of marshes where submerged food plants were abundant and cover plants not as dense as in nesting cover nearer the shores. In general, habitat improvement designed to produce better nesting conditions should simultaneously provide needed juvenile rearing cover. Very few of the areas under observation lacked sufficient rearing cover plants. Those areas which lacked the rearing cover plants were also deficient in nesting cover. The development of the rearing cover parallels the development of the nesting cover, which in turn is largely dependent upon a favorable water depth during the growing season.

Re-establishment of optimum plant cover on certain marshes depleted of vegetation from man's exploitations or from natural agencies, as abnormal water depths, fish, or muskrats, generally follows the establishment and maintenance of proper water conditions. Although a re-seeding or re-planting program in some instances may speed the establishment of cover plants on denuded marshes or on newly restored areas, natural reproduction from dormant seeds, wind, animal and water carried seeds, tubers and other repro-

ductive parts are usually sufficient to re-vegetate the marshes.

Rearing and nesting habitats maintained for waterfowl very often have additional wildlife values for species having the same or similar habitat requirements. Noteworthy among these additional values are fish, muskrats, mink and other semi-aquatic animals. However, conflicts between animals using the habitats should be settled in favor of the one for which the area is best suited. On waterfowl areas subordination of other animals is usually desirable. The taking and sale of surplus fur-bearers as muskrats and of predators as minks and snapping turtles will, however, defray part of the expenses of establishment and maintenance of duck-producing habitats.

FOOD PLANTS

As with the cover plants the key to the optimum growth and reproduction of food plants in Iowa marshes is proper water depth. No factor has a greater detrimental effect on the development of waterfowl food plants than does an extreme and irregular fluctuation of the water level. In general, however, submerged aquatics valuable as food were present in large amounts in all lakes and marshes frequented by redheads in the research area. Artificial propagation was not deemed necessary in any of the marshes of the research area. Manipulation of water depth to the favorable development of nesting and rearing cover plants is also conducive to the growth of important food plants.

Excessive numbers of fishes are known to have a detrimental effect on food plants. Parasitism of the valuable pondweeds and coontail by certain of the blue-green alga (*Anabena*, *Rivularia*) was observed in restricted parts of the research area. Thick blankets of green algae (*Cladophora*, *Pithophora*, and *Rhizoclonium*) covered acres of small shallow lakes shading to an injurious degree the submerged aquatic food plants.

Such plants as the bulrushes, bur-reeds and sedges served the multiple purposes of nesting cover, rearing cover, and food, whereas other plants, as smartweeds and arrowheads, were utilized mainly as rearing cover and food. The animal life, including snails, crustaceans, and adult and immature forms of insects thrived in the water having abundant cover and submerged aquatic plants. Optimum growth and development of many of these animals are favored by the presence of aquatic plants.

SUMMARY

To contribute to our knowledge of the bird and to assist in formulating management practices, the life history and ecology of the redhead, *Nyroca americana*, were investigated from March, 1938, to June, 1941, in Clay and Palo Alto counties, Iowa.

Northbound redheads reached the research area about March 20. Peaks of spring migration were noted March 21-25 and April 11-18, the latter dates representing the main flight. The yearly 3,000-4,000 migrant redheads preferred open water of the lakes

for resting at night, and bays of the lakes and large vegetated marshes were frequented in the daytime.

The sex ratio was 1.42 males to 1 female among 3,400 redheads.

Toward the latter part of April the mated ducks left the deeper water areas to seek nesting sites in the vegetation of the shallow marshes and sloughs. Marshes of 5 acres, or larger, situated not further than one-quarter mile from large permanent lakes were preferred nesting habitats. Although 28 other species of marsh-nesting birds were observed in the marshes, there appeared to be little conflict between them and redheads. Numbers of early nesting redheads as well as numbers of migrants were retarded by abnormally low temperatures during April and May, 1940. Nesting extended through 105 days, April 30 to August 12, 1940, a period of 28 days longer than in the two previous seasons. Late re-nesting attempts, initiated after previous nests were deserted because of a decline in water level, accounted for the extended 1940 nesting season. During the period May 8-24 the nesting season was at its height.

A total of 160 nests were under observation: 42 in 1938, 53 in 1939, and 65 in 1940. Calculated on the basis that 60 percent of the nests were found, during the average year on the 925 acres of vegetation available for nesting the average density was one nest to 10.6 acres. A high density of one nest to two acres was found on each of several small ponds in Dewey's Pasture.

Ninety of the 160 nests terminated successfully, 48 nests were deserted, and, of 22 destroyed nests, 12 were flooded, 4 destroyed by mink, 2 by crows, and 4 by unknown agents. Recession of water levels, particularly in 1940, caused desertion of 16 nests whereas a comparatively stable water level was correlated with the high percent (72 percent) of nest success in 1939. The apparent intolerance of the females to the laying of eggs in their nests by other ducks resulted in the desertion of 16 nests. The amount of promiscuous laying was inversely proportional to the nesting success and directly proportional to the fluctuation of the water level. The ruddy duck laid in 8.1 percent of the redheads' nests.

An average of 9.75 eggs was recorded for 115 complete clutches.

No definite rhythms of incubation was carried out by the female. An average of 17.6 hours a day was spent on the nest by one closely observed female during the 24-day incubation period. Hatching started June 1 and ended August 12 when the last nest, one of the 16 known re-nesting attempts, hatched. A total of 45.1 percent of the eggs produced young. Undeveloped eggs, probably infertile, represented 4.7 percent of the total eggs, while partially developed embryos left in the nest after normal hatching represented 5.5 percent of the eggs.

The most extensive nesting cover species were lake sedge (23 percent), narrow-leaved cattail (12 percent), hardstem bulrush (10 percent), and awned sedge (10 percent). The depth of the water in which

cover plants were located and proper interspersed and density of nesting cover were more important criteria in choice of nesting sites than was any preference which the ducks showed for any cover plant species. Nesting densities for the important cover plants were as follows: one nest to 3 acres of slender bulrush, one nest to 6 acres of hardstem bulrush, one nest to 11 acres of whitetop, one nest to 13 acres of sedge and one nest to 16 acres of narrow-leaved cattail.

Nests were built in marshes an average of 72 yards from the outer edge of marsh-vegetation, and 85 percent of the nests were located within 50 yards of open water. The nearest open water for 64 percent of the nests was around muskrat lodges. Nesting densities reached a maximum where not less than 10 percent and not more than 25 percent of the habitat was open water. Nests were constructed over water which averaged 11 inches in depth.

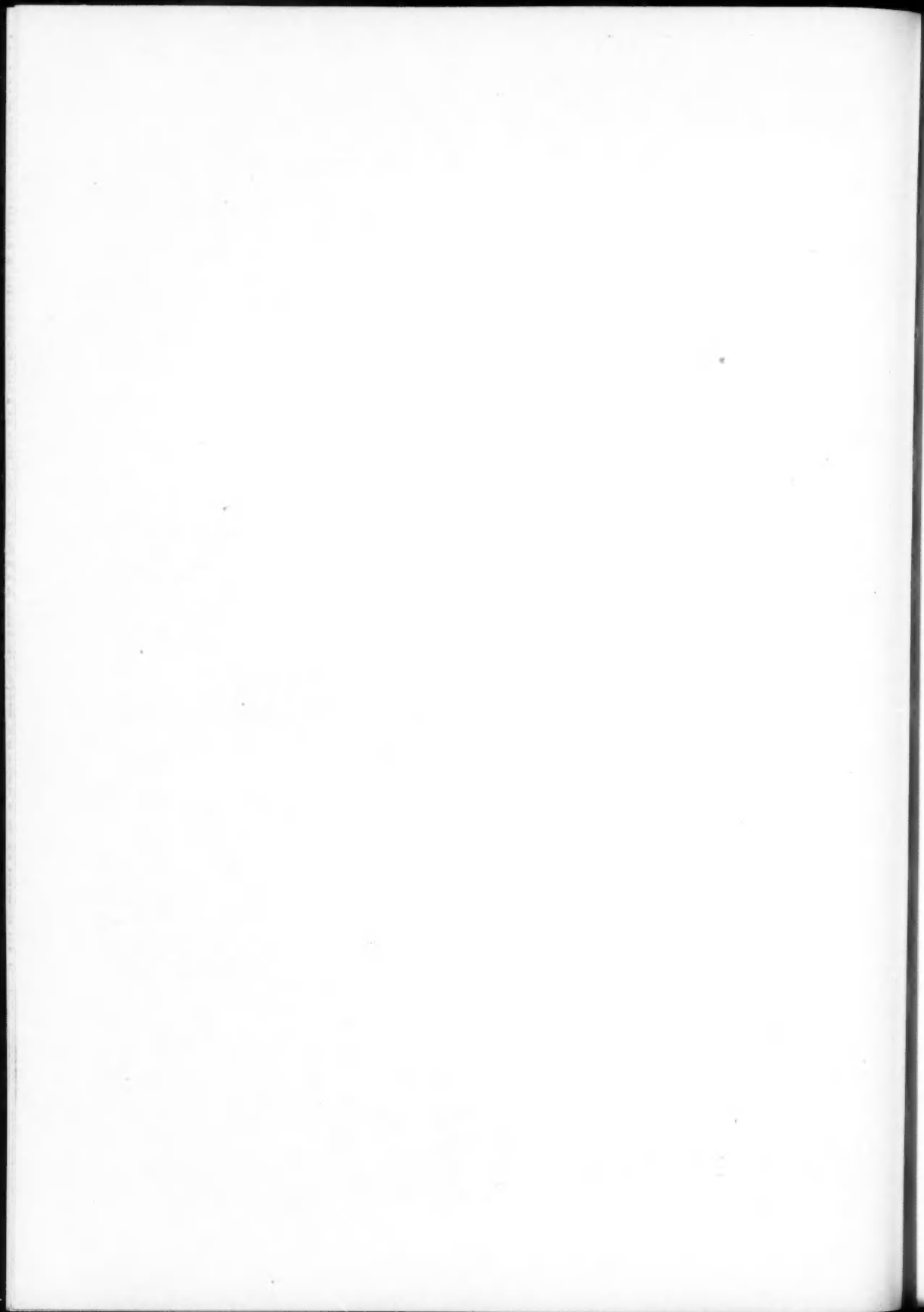
The Hardstem Bulrush—River bulrush—Burreed Community was most important as juvenile rearing cover. Brood counts showed that the greatest duckling mortality occurred during the first week of life. Evidence was noted of juvenile mortality from mink and snapping turtle predation, lead poisoning, exposure to weather, congenital disabilities, and trampling by the females of other young. The flight of the juveniles preceded the fall migration of northern redheads by nearly a month. An average of 6.3 juveniles of each brood survived, which represented a 70 percent survival of hatched young. Leeches parasitized 80 percent of the young redheads, but were not found to cause death.

Redheads were about five percent of the 1939 birds bagged by hunters.

Food plants essential to redheads were abundant in all marshes and in most of the lakes of the research area. Marshes under 25 acres in area should be protected from livestock. An adequate controlled water level is the most important factor to insure the production and utilization of cover and food plants by redheads.

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THE INFLUENCE OF TYPES OF SOIL UPON THE LOCAL DISTRIBUTION
OF SOME MAMMALS IN SOUTHWESTERN UTAH

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TABLE OF CONTENTS

	PAGE		PAGE
INTRODUCTION	73	FACTORS THAT INFLUENCE THE LOCAL	
GENERAL DESCRIPTION OF THE REGION	75	DISTRIBUTION OF THE PLANTS	91
METHODS OF STUDY	77	Climates	91
Soils	77	Barriers	91
Plants	78	Soil Water	91
Mammals	78	Soil Depth	92
DESCRIPTION OF FIELD STATIONS	78	Chemical Composition of Soil	92
Variation Between Stations	78	Gradient	93
Stations Studied	79	Slope Exposure	93
Soil Texture at Stations	82	Soil Texture	93
Soil Chemicals at Stations	82	Interaction Between Factors	93
THE ECOLOGIC ASSOCIATIONS OF THE AREA	83	DISTRIBUTION OF THE MAMMALS	95
Aerial Association	83	Local Races of Mammals in the Saint	
Riparian Associations	83	George Area	95
Populus-Salix Association	83	Comparative Abundance of the Species	96
Typha Association	83	Local Distribution of Certain Species	96
Tamarix Association	84	FACTORS THAT INFLUENCE LOCAL MAMMALIAN	
Distichlis Association	84	DISTRIBUTION	99
Pluchea Association	84	Climates	99
Upland Associations	84	Vegetation	99
Larrea-Franseria Association	84	Food	99
Larrea Association	86	Shelter	100
Cistoyneea-Larrea Association	87	Soil Texture	100
Emplectocladus Association	87	Soil Chemicals	101
Coleogyne Association	87	Soil Moisture	101
Atriplex-Hilaria Association	88	Soil Depth	102
Atriplex confertifolia Association	88	Gradient	102
Prosopis Association	89	Slope Exposure	102
Artemisia filifolia Association	90	Soil Color	102
Chrysothamnus Association	90	Barriers	103
		Speciation	104
		SUMMARY	105
		LITERATURE CITED	106

THE INFLUENCE OF TYPES OF SOIL UPON THE LOCAL DISTRIBUTION OF SOME MAMMALS IN SOUTHWESTERN UTAH

INTRODUCTION

Soils, through their various characteristics, directly and indirectly influence the distribution of plants and animals. This has long been realized by most biologists, but the task of accumulating exact data has been left until comparatively recent years. Merriam (1890:35) noticed the difference in plant life upon lava and that growing upon limestone in the Grand Canyon region. More recently, Shreve (1925:103) has stated that the local distribution of plants in the California deserts is "chiefly determined by the small differences in moisture conditions, such as are maintained by site, shading, or texture of the soil." Wells and Shunk (1931:502) in their study of the vegetation of the North Carolina Coastal Plain found that soil texture is of preeminent importance in the control of the vegetation of that area. Blair (1938:517) states that in the Bird Creek region of northeastern Oklahoma, in transition regions between associations, "edaphic factors determine to a large extent whether at any given place forest or grassland associations will occur." Larsen (1940:1) made texture and chemical analyses of soils in forests of northern Idaho and decided that edaphic conditions, to a large extent, control the order and stages of progression of the temporary types of forest plant life in that region. Smith (1940:452) analyzed soil textures on abandoned farmland in Oklahoma and arrived at similar conclusions regarding the important influence of soil in controlling plant succession. So intimate is the relationship between the soil and its plant cover that plants may be safely accepted as indicators of definite soil conditions (Clements 1920; Young 1936:133; Shantz 1938:835).

The relationship between soils and vertebrate animals is less well known but is undoubtedly for most species more complex than the relationship between soils and plants. Biologists in their field work frequently note the type of soil upon which particular terrestrial animals are taken, but detailed studies of the soil itself and of its effect upon animal life are comparatively few. A review of the numerous shorter notations of soil and mammal relationship or of most studies cannot be attempted here, but it will be of value to mention some of the important papers.

The color of soils seems to have been studied more intensively than any other one feature, and yet just a beginning has been made. According to most recent workers, there is a distinct correlation between the soil color and the pelage color of mammals living on that soil. Sumner (1921:75) and Sumner and Swarth (1924:81) seem not to agree with this idea although the relationship between pelage color in rodents and color of lava rock is recognized by more recent workers. Dark-colored races of rodents have

been described from lava beds by Dice (1929:2), Benson (1932:335), Blossom (1933:1), Burt (1939:1), and others. Bradt (1932:321) discussed the relationship between the dark color of mammals of the New Mexican Tularosa Malpais and the color of that lava bed. Blossom (1937:1) reported that the genera *Eutamias*, *Perognathus*, and *Ochotona* have developed dark-colored races on the dark-colored lavas of the Craters of the Moon in Idaho.

Dice (1929:1) described a very light-colored pocket-mouse from the white gypsum sands of New Mexico. Blossom (1933:1) described the race *Neotoma lepida auripila* and drew attention to the resemblance between its pinkish-buff coloration and the red rocks of its habitat.

Sumner (1926:182; 1932:70) gives some interesting photographs of three races of *Peromyscus polionotus* from Florida against their various soil backgrounds. A very light race, *P. p. leucocephalus*, has been developed on the white sands, which contrasts very strongly with the typical dark-colored *P. p. polionotus* from the dark sands.

Dice has shown in a series of studies that soil color and pelage color are closely correlated. In southern Arizona and California, he (1939a:20) found tendencies for dark-coloration on dark soils in the cactus-mouse, *Peromyscus eremicus*. He (1939:13) demonstrated that pelage color in the races of *Peromyscus maniculatus* in the Columbia Basin of Washington, Oregon, and Idaho was closely related to soil color. Dice (1940:8) demonstrated correlation between soils and pelage colors across North Dakota in the same species and (1941:3) showed that the light-colored mouse of the Nebraska sand hills region is lighter as a response to the light-colored soil.

Blair (1941:3) has shown a similar correlation between color of ground squirrels, *Citellus spilosoma major*, and soil color. Those on the white sands in the Tularosa Basin of New Mexico have larger and brighter white spots than those on darker soils fifteen miles distant.

Dice and Blossom (1937:102) demonstrated statistically this close relationship in colors of soils and mammalian pelage in the Sonora and Arizona region.

Benson (1933:1) investigated the color relationships of soils and mammals in the southwestern United States and demonstrated the importance of isolation. Dice (1940:419) found that on the Tularosa Malpais of southern New Mexico, where isolation is quite complete, the small mammals have evolved dark-colored races as a response to the dark backgrounds.

Mammals which are not isolated or are not found on extensive areas of soil of unusual color, have not differentiated enough to form dark, red, or light

rates. However, some individuals in such groups match their backgrounds. Osgood (1909:16) pointed out that dichromatic conditions exist in the genus *Peromyscus*. Goldman (1910:77) reported a similar condition for the genus *Neotoma* on the non-isolated lava beds near Saint George, Utah. Hardy (1941:90) reported concerning *Peromyscus crinitus* on these Saint George lava beds where, of 32 specimens, 15 are much darker than topotype material. This is as Dice and Blossom (1937:116) pointed out, that where isolation is not complete, some, but not all of the mammals will be dark. Hooper (1941:44) found incomplete isolation on the lava beds of Valencia County, New Mexico, where there were more dark rodents on the lava beds than on the nearby light-colored rocks.

This color relationship seems to be particularly close in regions where vegetation does not completely cover the soil. Stebler (1939:391) found that, with the genera *Neotoma* and *Eutamias* in the South Dakota badlands, "The correlation between pelage color and soil color seems to be most close in those habitats where the soil is exposed extensively through the lack of a heavy cover of vegetation."

The texture of the soil is also of importance. Stuart (1932:22) found a correlation between soil texture and the distribution of lizards in the Pahvant Valley of west-central Utah. This was likely related to the egg-laying habits of these reptiles. Grinnell (1932:311) stated that the distribution of a kangaroo-rat (*Dipodomys ingens*) seemed correlated with the distribution of Panoche fine sandy loam in interior California. Dale (1939:706) found that the kangaroo-rat (*Dipodomys heermanni saxatilis*) had adapted itself to a particular rocky type of environment and its distribution was controlled by the distribution of that physiographic feature. Landwer (MS.) reported that the kangaroo-rat (*Dipodomys ordii richardsonii*) in the Texas Panhandle was limited to sandy soils, that the prairie-dog (*Cynomys ludovicianus*) does not occur on sands, and that the ringtail-cat (*Bassariscus astutus* subsp.) and the juniper-mouse (*Peromyscus n. nasutus*) are more or less confined to rocky slopes. Osborn (1942:110) studied the distribution of prairie-dogs in relation to soils and concluded that the type of plant cover was of primary importance, but since he did not analyze coarse soils but only soils which were principally fine sands, the maxima and minima of soil tolerance of the rodents likely were not studied.

Soil texture, soil depth, and altitude have a direct relation to the size of pocket-gophers (*Thomomys*) in various parts of the western United States, according to Davis (1938a:338). He (1938:488) also states that in Texas the blackland prairies constitute an effective barrier to the dispersal of pocket-gophers (*Geomys*). Further studies of Davis (1940:6) suggest that *Geomys* is evidently dependent upon sandy soils for digging. Davis, Ramsey, and Arendale (1938:412) found that the distribution of gophers of the genus *Geomys* in Texas is correlated with the distribution of certain fine sandy loams over 4 inches

in depth. Hall (1941:233) attributes the development of the two species of *Microdipodops* to the adaptations of two populations, each to a different soil type.

This paper is a report of investigations on the concentration of salts in the soil, on the texture of the soil, on the color of the soil, and on the combined influence of these factors upon the distribution of mammals in the desert of southwestern Utah. Investigations were necessarily made of the effect of the various soil characteristics upon the distribution of the plants, which in their turn affect the distribution of mammals. The more direct relationships between the different soils and the distribution of mammalian species were also studied.

The collection of soil samples and of plant and animal specimens was made in the vicinity of Saint George, Utah, during the period from September, 1938 to September, 1941. Full time was spent on the problem from late May to mid-September during 1940 and 1941, but only intermittent collecting and analyses were made during the remainder of the period. Data from over 10,000 trap-nights for small mammals are included in the study. Field observations, chemical analyses to determine the saline content of the soils, and siftings to determine soil texture were carried out at Dixie Junior College at Saint George during the summers of 1940 and 1941.

Measurement of plant abundance on the various quadrats was made during April and May, 1941. The plant specimens collected were identified by comparison with material in the Dixie Junior College Herbarium. A majority of the plant specimens in this herbarium have been identified either by competent botanists from the larger universities or by authorities at the United States National Museum. The identification of the specimens of mammals and the writing of the report have been carried out at the Museum of Zoology, University of Michigan, during the period from September, 1941 to July, 1942 with revisions being made at Dixie Junior College during December 1943. Some soil samples and some specimens of small mammals have been deposited in the Museum of Zoology in addition to those retained in the writer's personal collection.

For his many suggestions and for his kindly advice, I wish to thank Dr. Lee R. Dice of the University of Michigan, under whose supervision the present study was conducted. For suggestions on taxonomic problems and the use of comparative material, I wish to thank Dr. William H. Burt of the University of Michigan. I also thank the following people for their help: Dr. A. M. Woodbury of the University of Utah for various altimeter readings in the area studied; Dr. W. F. Blair, Laboratory of Vertebrate Biology of the University of Michigan for checking certain *Peromyscus* skulls; Mr. B. P. Bole, Jr., of the Cleveland Museum of Natural History for the loan of certain *Dipodomys* skins from the Saint George area; Mr. Leslie Stromberg and Mr. Curtis L. Godfrey of the United States Soil Conservation Service at Saint George for field determinations of a few soils; Dr.

Remington Kellogg of the United States National Museum for comparing a series of *Perognathus formosus* skins with the type specimen; Dr. M. C. Sensi of the Geology Department of the University of Michigan for suggestions regarding the soils part of this manuscript; and Mr. M. J. Miles of the Dixie Junior College Chemistry Department at Saint George for many useful suggestions regarding the chemical analyses of the soils. The majority of the photographs were taken by Mr. Miles.

GENERAL DESCRIPTION OF THE REGION

The Saint George Basin and adjacent areas of southwestern Utah are varied in types of soil, in physiographic features, and in small mammalian forms adapted to desert conditions of life. It is presumed that the lack of a comparatively heavy plant cover in this arid region should cause these mammals to be adapted very closely to the soil substrate (Stebler 1939:391).

The area studied is located in Washington County, extreme southwestern Utah. Fourteen of the fifteen stations are within three miles of the city of Saint George. The fifteenth station is located west of the Beaverdam Mountains on the Beaverdam Slope about

one mile east of U. S. Highway 91 and one-half mile north of the Utah-Arizona state line on the old Wells-Fargo-Mormon Trail to California (Fig. 1).

All of the area studied lies in the Mohavian Biotic Province of Dice (1943:54). It is in Merriam's Lower Sonoran Life Zone, which is characterized by the presence of creosote-bush (*Larrea tridentata*) and its associates (Tidestrom 1925:9). It is part of the Western Desert Scrub Association of Clements (1920:170) although the presence of *Atriplex confertifolia* and similar plants shows affinities with Clement's Basin Sagebrush Association which is common at higher elevations about ten miles north of Saint George.

The chief topographical characteristic of the area is the broken, uneven surfaces created by the irregularly-shaped, brilliantly red and white colored Navajo sandstones and similar rocks. Large mesas that lead down from the north are usually flat-topped because of a capping of black lava. In many places, erosion has undermined this capping and scattered a jumble of boulders down the slopes. Where there is no lava the weathering has been even more rapid and numerous small canyons and gullies break the red hills. The entire area is highly eroded

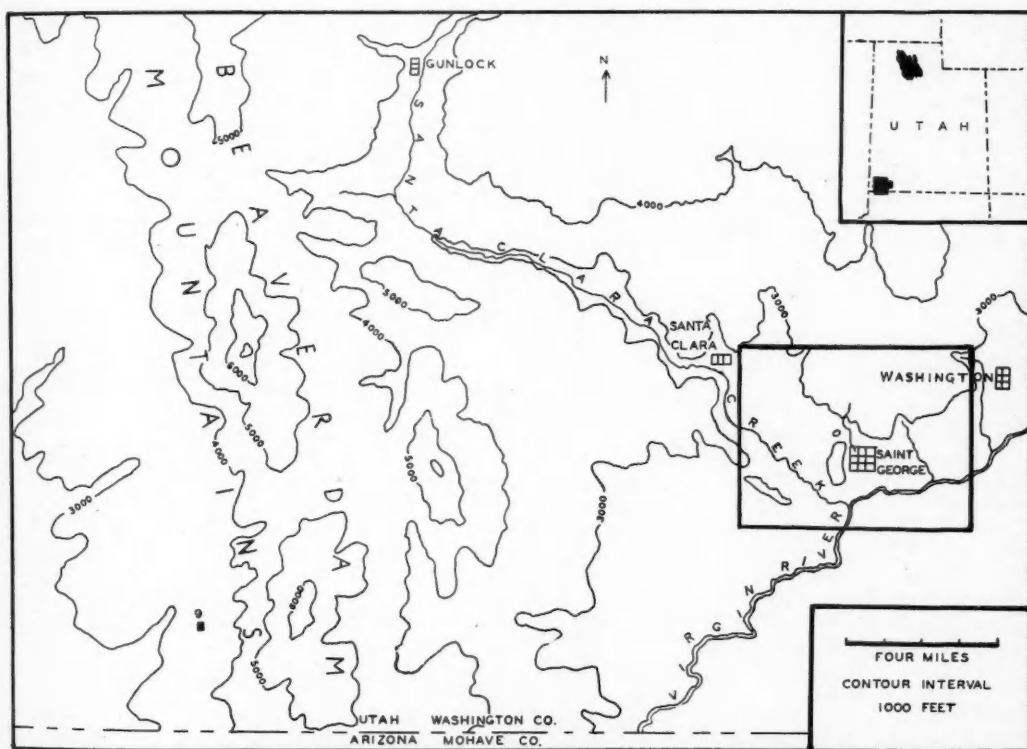


FIG. 1. Southwestern Washington County, Utah, showing location of the principal points discussed. Note Station 9 west of the Beaverdam Mountains. The area near Saint George (enclosed in a rectangle) is shown in Fig. 2. Contour numerals represent feet above sea level. Based upon map of the United States Geological Survey; the Saint George Quadrangle.

and hence has numerous kinds of surface and exposure. Collecting was done on most of the various surface types.

The city of Saint George, near which most of the field stations are located, is built upon a slope whose altitudes vary from about 2,730 to 2,950 feet above sea level. It is at the upper end of a gentle slope which leads south about two miles to the Virgin River. There are low foothills and mesas to the north, a mesa on the east and one on the west (Fig. 2). The Shivwits Plateau twenty miles to the south, the ramparts of Zion Canyon and the Hurricane Fault to the east, the higher Pine Valley Mountains (summit: 10,300 ft.) about fifteen miles northeast, and the rocky Beaverdam Mountains (summit: 7,300 ft.) twelve miles to the west entirely enclose the broad, though irregular, Saint George Basin in the Virgin River Valley of Utah.

The station with the lowest altitude (No. 7: 2,700 ft.) is located on a small bench near the confluence of the Virgin River and Santa Clara Creek. Another station (No. 12) is located on the top of the Black Ridge at 3,250 feet, while Station 16 is at 3,350 feet. Station 9 is on the Beaverdam Slope west of the Beaverdam Mountains at an elevation of 3,300 feet.

All other stations are intermediate between these extremes (Figs. 1, 2).

The desert climate in this area subjects the plants and animals to great extremes of temperature, to a high rate of evaporation, and to rainfall that is scanty and irregular. Alter (1941:1150) gives the average length of the growing season at Saint George as 196 days (137-234). The last killing frost in the spring is usually about April 10, and the latest date recorded was May 20. The earliest known killing frost in the autumn was September 25, and the average date is October 23. The prevailing winds are from the Mohave Desert areas to the southwest.

The temperature has an average daily variation throughout the year of thirty to forty degrees. The most extreme temperatures recorded (Alter, 1941: 1150) give an annual variation of 127° F. (-11° F. to 116° F.). The average, average minimum, and average maximum temperatures in degrees Fahrenheit, respectively, for the area are: January, 37.9° (23.1° to 53.3°); July, 82.5° (63.3° to 100.9°); annual, 59.4° (41.3° to 77.2°). Usually the nights are comparatively cool as a contrast to the extreme daytime heat, especially noticeable in the late spring and early summer months. During the winter, or from Novem-

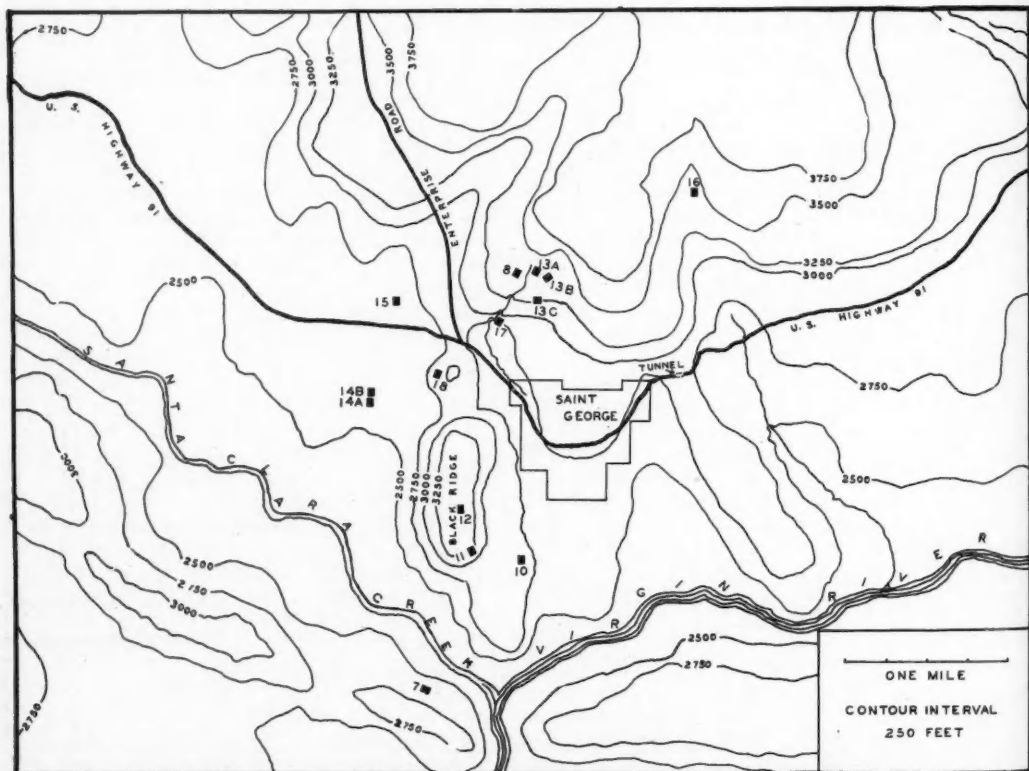


FIG. 2. Location of stations in the Saint George area. From the Saint George Quadrangle of the United States Geological Survey Maps.

ber to February, the daytime temperatures average low, occasionally being below freezing.

The average annual precipitation for forty years of record prior to 1931 is 8.73 inches (Alter 1941:1150). The least amount recorded in any one year is 3.55 inches (1894) while the greatest amount received in any year is 18.71 inches (1907). The month by month precipitation average for forty years of record for Saint George is: January, 0.93 inches; February, 1.11; March, 0.88; April, 0.54; May, 0.39; June, 0.22; July, 0.88; August, 0.95; September, 0.64; October, 0.78; November, 0.57; and December, 0.84 inches. The average number of days during the year when there is 0.01 inch or more of precipitation is forty-one (Alter 1931:14).

The average annual number of clear days varies from 180 to 220 (Alter 1941:742).

Frequently the entire year passes without snowfall. The average annual record of 6.0 inches for twenty-six years is made up of large snowfalls of irregular occurrence which usually melt soon after falling.

Alternating with the wet months of January-February and August-July are the two dry seasons of May-June and November. Irregularity of precipitation periods is characteristic. The summer precipitation usually falls in summer thunderstorms that may come suddenly and violently, causing washing and flooding of the soil. As a usual thing, the precipitation during winter months is spread over a number of weeks and falls gently, thoroughly soaking the ground.

An unusually wet season was recorded during the winter of 1940-1941. According to the Salt Lake office of the United States Weather Bureau as reported by the *Salt Lake Tribune* for March 6, 1941, "the accumulated precipitation from October 1, 1940 to March 1, 1941 was from 150-175% of the long time normal" in the Saint George area.

The most extreme cold weather known in this area since its settlement in 1862 occurred in January, 1937. A snowfall of over two feet followed by a long period of abnormally low temperatures (-11° F. compared to a previous all time low of -1° F.) produced havoc; nearly all plumbing in Saint George was frozen, many tourists were snowbound, and palm trees as well as many other exotic plants were killed. Cottam (1937:563), Woodbury (1938:484), and Turnage and Hinkley (1938:530) have described the effect of this cold period upon the native vegetation, which included serious frost injury to creosote-bush and mesquite.

METHODS OF STUDY

SOILS

Samples of soils from each of the field stations were examined and analyzed. Enough of each sample was collected to fill a one quart jar. Samples were collected from the surface two inches, from a depth of one foot, and at every foot thereafter to a depth of four feet. In some situations, on account of the presence of rock or hardpan, the samples were

taken at somewhat different levels. Where the soils were shallow, it was not possible to go as deep as four feet.

Texture analyses of the soils were made by dry sifting them through sieves of various sizes. In all, four divisions of each soil were made. About 400 gram portions of the original samples were first sifted through a screen with a half-inch mesh, and the part passing through was then passed successively through screens of 8, 20, and 80 mesh, respectively, per inch. Each soil portion passing through one screen, but not through the next smaller screen, was then weighed and its percentage of the weight of the sample which had passed through the one-half inch screen, was calculated.

Screening was continued until no more particles would fall through the screen being used. It was rather difficult to clean the screens without breaking some particles. Screens were cleaned by using a small brush and brushing the screen from below. Clays and other fine particles will tend to agglomerate and will give percentage readings similar, in many cases, to coarser soils. These finer particles can be determined only by sedimentation tests or some similar laboratory method, but it is believed that screening alone is more useful in the present study, for screening separates the soil particles in much the same way as does a digging rodent.

The data were entered in Table 2. Particles from the one-half inch mesh not passing through the one-eighth inch mesh are hereinafter referred to as "granule gravel." The next categories, in order, are "coarse sand," "fine sand," and "silt and clay." This classification is adapted from that of Wentworth (1922:377) and is not the same as that used by Youngs and other workers (1942:13) because the latter system of soil classification was not applicable since it does not consider particles larger than 2 mm. in diameter. However, the names of the soil series given in the descriptions are those of Youngs (1942:15).

The soils of this area, while commonly referred to as being "alkaline," are actually usually nearly neutral, as pointed out by Youngs *et al.* (1942:58). The term saline is probably more applicable.

Each sample of soil was analyzed for water soluble chlorides, sulphates, and carbonates and also for total carbonates. To dissolve the soil salts, the "Utah Method" of Harris (1920:86) was utilized. Fifty grams of soil were placed in 500 cc. of water and agitated vigorously for five minutes and then filtered under pressure. Portions of the filtrate were used in testing for anions of the soluble salts.

The chlorides were analyzed gravimetrically (Smith 1928:55). A sample of 100 cc. of the filtrate was acidified with nitric acid and an excess of silver nitrate was added. The precipitate was boiled and filtered, the ashless filter paper oxidized and the silver chloride accurately weighed. The chlorides were calculated as percentage of sodium chloride in the original soil sample.

Sulphate analysis was made on another 100 cc. of

the filtrate (Harris 1920:89) by acidifying with hydrochloric acid, heating and adding hot barium chloride. Similar filtering, burning of ashless filter paper and weighing gave data so that calculations could be made as if the sulphates were originally sodium sulphate, the common white "alkali" or Solonchek in this area.

Soluble carbonates were determined volumetrically (Smith 1928:116). The remainder of the filtrate from the original soil sample was titrated with hydrochloric acid standardized at 0.3 N, using methyl orange as the indicator. Calculations were made of the amount of sodium carbonate in the original soil sample. If any bicarbonates were present, they would be calculated as carbonate.

The total carbonates were determined by treating a soil sample weighing twelve grams with an excess of hydrochloric acid standardized at 1.4 normal. After all evolution of gas had ceased, the excess acid was titrated with standardized sodium hydroxide, using phenolphthalein as indicator. Because not only calcium, but also magnesium and other carbonates were presumed to be present, and since they were acted upon by the strong acid, the calculations were made as the percentage by weight of carbon dioxide evolved from the original soil sample.

Humus content in these soils is very low. Attempts were made to determine the amounts by incinerating soil samples of known weight, but some samples known to contain little humus gave very high values because of the evolution of carbon dioxide from carbonates. Although there is little humus, values for certain soils will be given where no carbonates were present to interfere.

The soil series named in the following discussion are from Youngs *et al.* (1942:15) who mapped most of the Virgin River area. Other field analyses of texture were made by Leslie Stromberg and Curtis L. Godfrey, of the Soil Conservation Service of the United States Department of Agriculture, who were stationed at Saint George in August, 1941.

PLANTS

Upon each field station, a quadrat (60 ft. by 60 ft.) was marked out by driving corner stakes. Upon this quadrat, the perennial plants were counted and the greatest width and height of each plant was measured. From these data was calculated the number of plants per acre. The results of this census are given in tables in the description of the ecologic associations. No count was made of the multitudinous annuals, but an effort was made to list them in their order of abundance. Five grades of frequency are employed. In order, from the most numerous to the least, these are: abundant, common, moderate, scarce, and rare.

MAMMALS

Trapping for small mammals was carried on at the field stations at varying periods and seasons from September, 1938 until July, 1941. Small steel traps, rat traps, "Museum Special" traps, and various types

of metal box traps were used. During the first two years, the traps were baited both morning and evening, but during the later periods of the study, no trapping was done for the diurnal ground-squirrels. Oatmeal served as bait for all rodents taken. The scientific names of the carnivores are, for the most part, those given by Presnall (1938:8) for the mammals of the lower desert regions of Zion National Park, which is located 54 miles to the eastward, since only a small number of these animals was observed or trapped. In the description of the several ecologic communities the attempt is made to list the mammals in order of abundance, using the same scale of terms as is employed in the comparison of the annual plants.

In an effort to check on previous trapping records and to determine the relative abundance of small nocturnal mammals, two trap lines were set for three consecutive nights at each field station. One line consisted of fifty "Museum Special" snap traps in a straight line ten yards apart. The second line, with the traps placed fifteen yards apart, was distant enough so that the two lines would not duplicate any area. This line consisted of twenty metal traps of the type described by Blair (1941:191) designed to capture animals alive so that they could be marked and released. All of this trapping was done during a dry period between May 30 and July 24, 1941. The results are given in Table 14.

DESCRIPTION OF FIELD STATIONS

VARIATION BETWEEN FIELD STATIONS

The parent soil-forming materials in the Saint George Basin are unusually varied. They include red, buff, yellow, and white sandstones as well as vari-colored shales, conglomerates, gypsum, limestones, black basalt, volcanic cinders, and gray granite. Clays are somewhat unusual in this region, hence most of the soils studied are sands, sandy loams, or gravels produced by weathering of the commoner sandstones and of a few limestones. With the exception of the lava rock, covered by a brownish-black "desert varnish," most of the rocks and soils included in the study have a more or less red color. However, a few of the Saint George and the Beaverdam Slope soils have a light brown or buffy color, and often include particles of gray or brown gravel.

From the geological point of view, as shown by Gardner (1941:245), the Beaverdam Slope soils are recent in origin, belonging to the Basin-and-Range Physiographic Province, characterized by Quaternary and Tertiary alluvial deposits. The soils of the Saint George Basin, on the other hand, are formed from older Jurassic rocks, the area belonging to the Colorado Plateau Physiographic Province.

A hard-baked surface is characteristic of most of the soils. Because of the scanty rainfall and the long-continued summer heat, only a few of the coarser sands fail to bake hard on top. This top crust is usually over one-half inch in thickness, but there is considerable variation. The hard pounding of the

summer thundershowers washes away many of the finer soil particles and leaves small gravel pieces exposed to form a "desert pavement" on most areas. Most rodent burrows are located in the shelter of a bush or similar place where the top crust is not so hard as it is between the widely spaced desert shrubs.

Each of the fifteen stations was located on an area of a definite type of soil and within one ecologic association, although a few, such as those restricted to a narrow canyon bottom or along a wash are small and surrounded by other ecologic associations. Each of the field stations was large enough to allow two trap lines to be set simultaneously. One trap line was five hundred feet while the other was three hundred feet in length. Each station contained a marked quadrat (60 ft. by 60 ft.) on which the plant counts were made and from which the soil samples were taken.

FIELD STATIONS STUDIED

Station 7 is on a small terrace southwest of Santa Clara Creek and north of the Virgin River near their point of junction two and one-half miles south of Saint George. This terrace is about 300 ft. by 1,200 ft., comparatively smooth and slopes east 2.6%.

The soil at Station 7 was mapped by Youngs *et al.* (1942:28) as Moffat fine sandy loam. This is a comparatively coarse-textured soil of intermediate age with a variable but definite lime concentration in the subsoil and with a fairly good moisture-holding capacity. The top fifteen to twenty inches is light brownish-red in color and contains minute crystals of calcite and has small pebbles in the top crust. Fine sandy clay loam, almost white in color, forms much of the subsoil.

There is little or no sulphates or chlorides except at four feet or below. The total carbonate present is fairly high but only a small amount is in water-soluble form. Stratification in the subsoils causes the great variation in total carbonates shown in Table 3.

Station 7 is heavily overgrazed in the spring and the soil is hard-packed by sheep.

Station 8 is on the north side of Watereress Springs about one mile northwest of Saint George and slopes southwest 19.2%. Some trapping was done on each side of a ridge which juts out from the main hillside.

This station is almost covered by small, bright red sandstone rocks, many of which are thin and flattened fragments, but larger pieces and boulders of this sandstone also occur. Red sandstone ledges from 1 ft. to 15 ft. high run horizontally parallel through the area. North, near the top of the hill, one ledge is about one hundred feet high. This soil was not named by Youngs as it is rough, stony land unfit for agricultural use.

This soil, which varies from about three inches to a foot in depth, comes entirely from the underlying red sandstone. Only one soil sample was analyzed as the material seemed rather uniform in quality and texture. This sample contained a small amount of

sodium sulphate and some carbonate, very little of the latter being in a water-soluble form.

Station 9 is on a broad, alluvial, gravel fan about thirty miles southwest of Saint George on the Beaverdam Slope. This area is cut by rock-filled gullies four to twelve feet deep which vary from twenty to two hundred feet in width. It is about seven miles from the Beaverdam Wash and slopes 8.3% southwest.

The light buffy brown surface soil, after removal of large gravel, is fine sandy loam. The soil from one foot in depth is fine gravelly loam which is only slightly lighter in color than the top soil. Deeper soils are fine limestone gravel, mixed black, gray, and white in color. This belongs to an, as yet, unmapped series of soils.

Particles of angular-shaped gravel project above the baked surface of the fine sandy loam. Occasionally larger boulders are exposed, but these are more common in the washes where the bottoms are covered with loose gravel and larger rocks. The banks of such washes show that the horizons deeper than two feet are of close-packed gravel and conglomerate.

The soil at Station 9 becomes coarser with depth. There is but a shallow soil upon a gravel base. The gravel removed by the one-half inch mesh amounted to 23.4% by weight of the total sample of topsoil. There is comparatively little coarse sand and small gravel, the soil being composed mainly of larger gravels interspersed with fine sandy particles.

The total carbonate present increases with depth, but the soluble carbonates are in slightly greater concentration at a depth of one foot than in the deeper gravels. The soluble chlorides and sulphates have probably been leached out of the surface layers but are present in the deeper gravels where they occasionally form white lines of crystals on exposed banks.

Station 10 is east and north of the Saint George Airport on the lowest terrace of the lava-capped Black Ridge. Recently the airport has been enlarged and most of the original station has been cleared for landing purposes, but a small area covered with Larrea and associates remains east of the flying field. The general slope is 2.8% south.

The soil at this station has been classified (Youngs 1942:38) as belonging to the shallow, gravelly soils which are among the oldest in the region. It is a shallow phase of the Harrisburg stony loam which is very light reddish in color, contains many boulders and has a low water-holding capacity. At slightly over one foot down there is a "caliche" of nearly white lime carbonate, a hardpan with much embedded gravel and stone. During the dry season, there is a thin crust with many white pebbles on the surface.

The water-soluble carbonate, because of the action of evaporating soil moisture, is slightly more concentrated on the surface than below. This soil becomes rapidly coarser with depth.

Station 11 is north of the Saint George Airport on the rocky slope of the upper mesa where the gradient is 43.2% to the south. This Black Ridge is

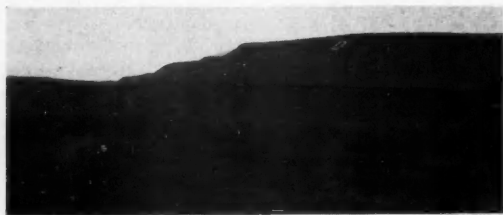


FIG. 3. The Black Ridge west of Saint George. Station 10 is located upon the lower terrace to the left; Station 11 is on the steep hillside left of the Dixie College emblem, the "D"; while Station 12 is upon the highest terrace above the "D."

so named because of numerous, large (1 ft. to 10 ft.), black lava boulders on these slopes. There is very little soil between or upon these boulders, hence samples were not taken from deeper than nine inches. This soil is reddish in color but contains numerous small black lava pebbles.

The total carbonates present in the topsoil is about the same as at Station 10, but the amount of soluble carbonate is less, probably because the steep slope offers better drainage for its removal.

Station 12 is on the highest terrace of the Black Ridge above and north of Station 11. This lava-capped area is much like the lower terrace. The gradient is 2.8% to the south, except at the edge of the mesa where there is a variation from 4% to 10%. The mesa varies from 400 to 500 ft. in width and is about one-half mile long.

The soil at Station 12 is shallow Harrisburg stony loam. The topsoil, pale reddish in color, contains a greater quantity of angular white gravel and large rocks and is not so fine as that from Station 10. The "caliche" is about ten inches beneath the surface. The analyses suggest the white pebbles may be limestone, for the total amount of carbonate in this topsoil (13.58% CO_2) is greater than at Station 10, although the amount readily soluble in water is less. At Station 12, there is a smaller proportion (32.1%) of silt and clay than is found in the Harrisburg stony loam from Stations 10 (45.6%) or 16 (42.9%) (Table 2).

Station 13a is near Watercress Springs southeast of Station 8. The area slopes west 11.4% and is over one-fourth mile long, but it is narrow, never being more than 250 feet from a vertically-walled wash which bisects the area. The sides of this wash show that the soil is from eight to twelve feet deep, underlain by a firm sheet of red sandstone.

This soil is Saint George fine sand (Youngs 1942:46), a recently formed alluvial soil. At this point it is nearly black in color and contains large amounts of organic matter, being higher in humus content than any other soil analyzed. The soil becomes lighter in color with depth, being a pale gray at four feet. There are white flecks of lime in the subsoil which cause a variation in the salt analysis. Sometimes red tints appear in this soil because of

inwashing of slight amounts of the neighboring red sandstone.

The Saint George fine sands were formed under conditions of poor drainage. Although usually low, the ground water level probably varies at different periods during the year. The nearby Watercress Springs flows throughout the year and numerous small "seeps" in the nearby wash show the continued presence of soil water.

Thoroughly oven-dried surface quartz sand from this station lost 8.15% by weight when burned. Part of this loss may have been because of the 1.13% carbon dioxide present in the form of carbonate, but the remainder of the loss was likely because of organic material. The values lost by incineration of subsoils were: one foot, 3.9%; two feet, 3.38%; three feet, 3.73%; and four feet, 7.72%. In each case, less than 2% of this loss could have been because of carbonates (Table 3).

A thin crust over the loose sand was likely formed by the crystallization of salts left by evaporation of soil water after each rainfall. This soil is fine and fairly uniform in texture becoming only slightly coarser with depth.

The salt content of the soil is high (Table 3). Although the amount varies in each little spot, it is everywhere more than 0.5% and hence to be considered as strongly saline. In one bare spot at the edge of this station, analysis of the thick crystalline crust showed 0.04% soluble carbonate, 5.82% sodium chloride, and 24.56% sodium sulphate—surely enough to prohibit the growth of even the most saline loving plants! However, this is unusual for any except small areas. The values reported in Table 3 more nearly approach the average conditions where *Pluchea* and *Dondia* grow.

Station 13b is near Watercress Springs south of and adjacent to Station 13a. The ground slopes north 4.1%. The somewhat circular-shaped area is about 800 feet in diameter and surrounded by ledges and steep hillsides of red sandstone. Two small washes, each about five feet deep, run parallel through the area.

This soil at Station 13b, about six feet deep, is Saint George fine sand. It has a blackish-red color because it probably was formed under better drainage conditions than was the soil at Station 13a. The subsoil at Station 13b is a deeper, brighter red color than the surface material. There is less than one-fourth of the organic material found at Station 13a. There are almost no salts in the surface soil, although they occur in the subsoils. The topsoil bakes into a crust, although this is not as firm and definite as at Station 13a.

Station 13c is in the same canyon as the last two stations, being on the hillside west of Station 13b and southwest of 13a. It is directly south of Station 8 which it much resembles, being on a rocky hillside of the same kind of red sandstone. This rough stony land slopes east 16.6%.

The soil at Station 13c is less saline than at Station 8 as there is no soluble sulphates and they contain

less total carbonates. The soil is also more shallow than at Station 8, the plants in many places growing out of cracks in the red sandstone. The soil is usually less than six inches in depth, being composed mainly of numerous small, bright-red sandstone chips.

Stations 14a and 14b, in a region of varying but similar soils, are west of the Black Ridge about one-half mile south of U. S. Highway 91 near the road which leads southwest to the Santa Clara Fields. East of these stations, more than a quarter of a mile, is the Black Ridge, while Santa Clara Creek is west about the same distance. The general gradient is southwest 1.8%, but there is great variation in the irregular, broken area where numerous small furrows and washes are but one or two feet deep.

At these stations, the shallow, residual soils are very much like the Purgatory series of Washington County, but are deeper and in a more advanced stage of soil formation than the soils of that series. Where the topsoil has been entirely removed and the underlying gypsum eroded, the area is covered principally by *Atriplex confertifolia*. Such areas are designated as 14a. The slightly higher, sandy ridges, very irregular in shape and size, are covered mostly with *Hymenoclea salsola*. These are designated as 14b. The plant cover on these gypsum soils is light as would be expected (Campbell & Campbell 1938:572).

At Station 14a, erosion and deposition have acted alternately upon the numerous small basins and ridges and have left soils of variable appearance. The parent material is mostly a dirty gypsum and the white to red color of the soil depends upon how much of the gypsum has dissolved and what proportion of the red siliceous material has been left.

The surface is fine sand with a soft friable structure, the subsoil from three to ten inches is clay, and from six to fifteen inches (average about ten inches) deep there is a gypsum hardpan. In some places there are two soils, one upon the other, separated by a very thin hardpan. Each layer independently becomes coarser and more saline with depth. In some places the material below ten inches is a fine sandy clay, about the same as the subsoil at Station 14b, but in other places the upper subsoil is a soft spongy mass of rose, maroon or white gypsum, which is usually more cemented in deeper layers. The soil at Station 14a is much finer than at 14b. At Station 14a, part of the surface crust found during the dry season is actually a thin, dried, darkened coating of mosses and lichens which covers almost the entire surface with a vivid green during the rainy season.

The topsoil at Station 14b is fine sand which extends to a depth of six or eight inches and gives way to a horizon of sandy clay loam with a great concentration of gypsum, below which (varying from two to three ft.) is a gypsum hardpan. The chief soluble salt is a sulphate which is not as concentrated on the surface as at Station 14a. The colors vary, but most of the surface is slightly redder than at Station 14a, resembling the soil color at Station 13c. The deeper horizons are mostly white with rose or maroon flecks.

Station 15 is one-quarter mile west of the north end of the Black Ridge on a sandy flat between two small, low, black lava ridges north of U. S. Highway 91. This flat measures about 800 feet by one-fourth mile and slopes south 2.8%.

The soil at Station 15 is Tobler fine sandy loam (Youngs 1942:22), one of the deep, fine-textured, alluvial soils of recent formation peculiar to this valley. It is formed of outwash from the red sandstones and shales and hence is redder than many of the other soils in this area, being a salmon-pink color. The surface and subsoils are rather uniform in texture and practically no alkaline forming or calcareous materials are present. There is a surface veneer of loose, drifting, fine sand usually less than one inch in depth.

Station 16 is east of the former Saint George-Enterprise road, one-half mile north of the Middleton Tunnel on U. S. Highway 91, about two miles northeast of Saint George. It is upon a high, lava-capped mesa, being nearly the same altitude as Station 12. The area slopes south 4.1% and is on a flat over one-half by one mile in extent.

The topsoil at Station 16 is Harrisburg gravelly fine sandy loam which is similar in color but not so shallow as the soils at Stations 10 and 12. This soil has somewhat the same texture as that from Station 10, but does not have as many large stones. The horizon to about fifteen inches is a white, gravelly clay loam. As with most soils, the total carbonates present increase with depth. There are no chlorides or sulphates present.

Station 17 is west, downstream from Station 13a and is northeast of the Black Ridge. The gradient is southeast 4.4%. The area studied was about 600 feet by 800 feet, but recently a brush fire has burned most of the mesquite from the north half.

There are no harmful "alkalis" and but slight concentrations of carbonates in this soil. The bank of the nearby wash showed a vertical distance of 14 feet 4 inches of a uniform appearing layer of Saint George fine sand. The soil is redder than at Station 13a, being about the same as at 13b. The subsoils from three and four feet are darker and grayer than the topsoils.

Station 18 is on the lower slope of the northwest tip of the Black Ridge southeast of Station 15. From the base of the hill to the first flat upon the mesa is about 250 feet. The area trapped is about one-fourth mile long, the traps being placed parallel with the top of the mesa halfway up the slope. The gradient is 29.2% northwest.

At Station 18, the surface is almost entirely covered with dark brown and gray lava rocks which are less than one foot in diameter. Some of these rocks are covered with a glittering "desert varnish" and seem to be limited almost entirely to the surface, there being very few rocks below. These surface rocks and the accompanying black gravel have undoubtedly been carried down the slope from the lava layer at the summit of the mesa.

Gravelly light clay loam is found between the rocks

at this station. The surface soil is similar in color to the sand at Station 13c, but black lava gravel is mixed with it. The soil gets heavier and the total carbonates increase with depth. There are also sulphates and chlorides in the gravelly clay loam subsoils, which contain varying amounts of lime and differ in the shades of pink and garnet shown. This soil is related to the Moffat series of soils, such as at Station 7, but is redder and heavier in texture.

SOIL TEXTURE AT FIELD STATIONS

These fifteen stations may be divided into three main groups upon the basis of the kinds of topsoil present. Group I (Stations 8, 10, 11, 12, 13c, and 18) include those areas where large stones or boulders are numerous over the ground surface. The few stones found on the surface at Stations 9 and 16 are neither as large nor as numerous as those found elsewhere, hence these two stations are included with Station 7 in Group II: gravelly soils with more than five per cent of their particles of granule gravel. Group III (Stations 13a, 13b, 14a, 14b, 15, and 17) includes those stations with less than three per cent granule gravel.

In Group I (stony soils) the percentage of granule gravel in the topsoil varies almost directly with the gradient of the area, probably because the sand and smaller particles are easily carried away by water from summer thundershowers. The following table illustrates this:

TABLE 2. Depth in inches and texture in percentages by weight of 400 gram soil samples from fifteen stations in the Saint George, Utah, area. The texture as reported in this table was determined entirely by the dry sifting method. Granule gravel contains particles smaller than $\frac{1}{2}$ inch and larger than the 8-mesh per inch sieve; coarse sand: 8 to 20 mesh size; fine sand: 20 to 80 mesh size, and silt and clay smaller than 80 mesh. Adapted from Wentworth (1922: 377).

Field station, No.	11	18	8	13c	12	10	16	9	7	14a	14b	13a	13b	17	15
Depth in inches	9	48+	8	5	10	12	20	30	48+	21	30	120	72	172	48+
Texture of topsoil:															
Granule gravel	31.3	23.1	19.8	13.9	7.6	9.6	9.5	19.8	11.3	00.0	00.5	00.0	3.0	00.2	00.2
Coarse sand	8.9	15.2	15.0	6.2	8.4	7.3	11.6	10.0	9.5	2.1	00.5	00.4	2.5	00.1	00.1
Fine sand	20.2	27.6	31.8	40.9	51.9	37.5	36.0	21.6	38.0	23.5	49.4	47.2	23.0	50.3	65.8
Silt and clay	39.6	34.1	33.4	39.0	32.1	45.6	42.9	48.6	41.2	74.4	49.6	52.4	71.5	49.4	33.9
Texture of soil from near one foot depth:															
Granule gravel	13.9	20.3	5.6	15.8	5.4	35.7	4.5	00.0	00.1	00.0	5.5	00.0	00.0
Coarse sand	14.9	22.0	13.1	18.3	14.4	7.9	6.6	2.4	1.4	00.3	3.7	00.0	00.0
Fine sand	40.8	26.6	53.2	35.9	36.0	15.3	37.5	33.1	51.1	48.1	26.5	48.7	57.9
Silt and clay	30.4	31.1	28.1	30.0	44.2	41.1	51.4	64.5	47.4	51.6	64.3	51.3	42.1
Texture of soil from near two foot depth:															
Granule gravel	27.7	26.0	49.3	15.4	00.2	00.4	00.0	3.5	00.0	00.0
Coarse sand	22.4	16.5	26.0	38.1	11.5	4.0	00.1	3.8	00.2	1.1
Fine sand	25.3	39.1	15.8	27.2	38.8	50.5	52.2	24.4	55.4	61.1
Silt and clay	24.6	18.4	8.9	19.3	49.5	45.1	47.7	68.3	44.4	37.8
Texture of soil from near three foot depth:															
Granule gravel	24.4	41.0	12.3	00.0	1.2	00.0	00.0
Coarse sand	22.1	20.7	13.8	00.1	1.6	2.2	00.7
Fine sand	28.3	22.7	37.6	54.4	34.8	54.7	58.8
Silt and clay	25.2	15.6	36.3	45.5	62.4	43.1	40.5
Texture of soil from near four foot depth:															
Granule gravel	40.5	20.4	00.0	00.5	00.0	00.5
Coarse sand	23.6	23.9	1.6	1.5	00.3	1.0
Fine sand	21.9	34.5	57.8	29.5	47.2	70.0
Silt and clay	14.0	21.2	40.6	68.5	52.5	28.5

TABLE 1

Station	11	18	8	13c	10	12
Gradient (Percentage)...	43.2	29.2	19.2	16.6	2.8	2.8
Percentage of granule gravel in the topsoil...	31.3	23.1	19.8	13.9	9.6	7.6

The soils of Group III (fine soils) can be separated into the saline and shallow (14a, 14b), the saline and deep (13a, 13b), and the non-saline and deep (17) fine sands. Soil from Station 15 of Group III is a non-saline and deep fine sandy loam. These six stations are all comparatively level, none of them having a steep slope.

SOIL CHEMICALS AT FIELD STATIONS

Five of these fifteen stations are strongly saline, according to the terminology of Youngs *et al.* (1942: 60) when the chlorides and sulphates are considered jointly (Table 3). In order of decreasing salinity from first to last, these are Stations 13a, 14a, 14b, 13b, and 18. The remaining ten stations are considered as salt free or nearly so.

The soil of all these stations contains lime, which accounts for the common "caliche" on many of them. This chemical seemingly does not directly have a great influence upon the plants, at least not to the same extent as do the sulphates and chlorides.

TABLE 3. Salts in soils from fifteen stations in the Saint George, Utah, area. Water soluble chlorides are stated as percentage by weight of sodium chloride present in original soil sample of fifty grams; water soluble sulphates as sodium sulphate; water soluble carbonates as sodium carbonate; and total carbonates as carbon dioxide.

Field station, No.	11	18	8	13c	12	10	16	9	7	14a	14b	13a	13b	17	15
Percentage of sodium chloride in:															
Topsoil	0.00	Trace	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00
One foot depth	0.00	0.89			0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Two foot depth		0.00					0.00	0.05	0.00	0.00	0.00	0.00	0.15	0.00	0.00
Three foot depth		0.23							0.00			0.10	0.06	0.00	0.00
Four foot depth		0.19							0.01			0.11	0.09	0.00	0.00
Percentage of sodium sulphate in:															
Topsoil	0.00	Trace	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.57	Trace	5.83	Trace	0.00	0.00
One foot depth	0.00	0.00			0.00	0.00	0.00	0.00	0.00	5.03	Trace	1.80	0.00	0.00	0.00
Two foot depth		0.00					0.00	0.06	0.00	5.69	4.67	2.34	0.66	0.00	0.00
Three foot depth		0.44							0.00			6.35	0.52	0.00	0.00
Four foot depth		0.24							0.07			2.58	0.40	0.12	0.00
Percentage of sodium carbonate in:															
Topsoil	0.01	0.02	0.00	0.00	0.01	0.02	0.01	0.01	0.01	0.01	0.01	0.04	0.00	0.01	0.00
One foot depth	0.01	0.01			0.01	0.01	0.01	0.02	0.01	0.01	0.03	0.03	0.01	0.03	0.01
Two foot depth		0.02					0.01	0.01	0.02	0.01	0.02	0.02	0.01	0.01	0.02
Three foot depth		0.03							0.02		0.01	0.03	0.01	0.01	0.01
Four foot depth		0.01							0.01			0.01	0.02	0.03	0.01
Percentage of carbon dioxide released by acid (total carbonates) in:															
Topsoil	6.31	2.76	4.77	1.77	13.58	6.70	6.50	17.52	6.57	3.15	3.30	1.13	1.94	Trace	0.00
One foot depth	6.61	5.89			13.00	13.71	11.35	19.50	5.53	1.67	11.52	1.42	1.72	0.18	0.05
Two foot depth		10.46					22.64	45.14	25.94	1.72	13.49	1.83	1.96	0.34	0.61
Three foot depth		6.54							17.60		3.49	2.24	1.72	2.56	0.60
Four foot depth		10.47							25.45			9.70	2.52	1.79	0.63

THE ECOLOGIC ASSOCIATIONS OF THE AREA

Sixteen ecologic associations of the Lower Sonoran Life Belt near Saint George are here described. Other associations will likely be recognized after further study. Except for the Aerial Association, those listed here may be broadly divided into two groups: riparian and upland. With the exception of Station 13a, which was located in a riparian association, the present study was confined to the upland types. The term "association" as used here refers to any assemblage of plants and animals with general uniformity in taxonomic composition and in ecological organization which over a period of time occupies an area with more or less definite geographic limits. Thus it is a special type of community held together primarily by the environment (Alverdes 1927:4; Woodbury 1933:167). The term is used for both the climax type of plant life and for the well-marked successional stages (Dice 1943:4).

The plants and animals here listed as members of each of these associations have been determined only on areas east of the Beaverdam Mountains. Only the *Clistoynece-Larrea* and the *Emplectocladus* Associations were studied west of the Beaverdam Mountains.

The plants of each association are listed in the approximate order of their abundance and probable importance rather than in their proper taxonomic sequence. Except for the name *Larrea tridentata* (= *Covillea tridentata*), all scientific plant names are those given by Tidestrom (1925).

AERIAL ASSOCIATION

The Aerial Association includes at least eleven species of bats which are known to forage for food over these areas. The abundant species are *Pipistrellus h. hesperus*, *Eptesicus fuscus pallidus*, and *Tadarida mexicana*. *Myotis subulatus melanorhinus* and *Antrozous pallidus cantwelli* are common while only a few *Myotis y. yumanensis*, *Myotis californicus pallidus*, *Lasionycteris noctivagans*, *Lasiurus cinereus*, and *Lasiurus borealis teliotis* are found. A rare species is *Tadarida macrotis*. Some of these species are found only periodically, probably being migratory through this region. Records of these bats have been published separately (Hardy 1941:289).

RIPIARIAN ASSOCIATIONS

Populus-Salix Association.—This association, common along streams and irrigation canals, is characterized by the Fremont Cottonwood (*Populus fremonti*) with which grow willows, mints, grasses, and similar moisture-loving plants. Many of these forms seem to have followed water down from higher elevations. The hoary bat (*Lasiurus cinereus*) has been taken from the limbs of trees during the summer, but no other species of mammal has been collected.

Typha Association.—This association, mostly limited to areas near the Virgin River and Santa Clara Creek, is characterized by the common cattail (*Typha latifolia*) and a number of species of sedges and rushes. The type locality of the Utah meadow-mouse (*Microtus montanus rivularis*) and the Virgin Valley

muskrat (*Ondatra zibethica goldmani*) is in these marshes along the Virgin River near Saint George. The Nevada weasel (*Mustela frenata nevadensis*) and the desert harvest mouse (*Reithrodontomys m. megalotis*) are also known from this association, where the latter builds its nest of fibers in cattails above the water line.

Tamarix Association.—This is characterized by heavy stands of *Tamarix gallica*, usually found in riverwash of the Virgin River flood plains. The sandy soil beneath these trees supports comparatively little plant life. The Great Basin skunk (*Mephitis mephitis major*) frequently hunts here. Long (1940: 176) reported the presence of *Dipodomys merriami* in this association at Saint George. *Peromyscus eremicus eremicus* and *Peromyscus maniculatus sonoriensis* have been trapped in this association.

Distichlis Association.—This is confined to comparatively small areas where the salinity of the soil is high, where water is present in the soil, and where the drainage is rather poor. This short, sharp-leaved saltgrass (*Distichlis spicata*) covers the ground as a thick mat, but in some places yerba mansa (*Anemopsis californica*) is able to spread through the turf. Occasionally the runways of *Microtus montanus rivularis* are found in the thick beds of this grass.

Pluchea Association.—This follows watercourses where soils are deep and saline and small amounts of moisture exist in the subsoil. The arrowweed (*Pluchea sericea*) is a perennial, willow-like composite which usually produces a thick stand of slender limbs three or four feet high. In the more alkaline areas, *Dondia* sp. may be mixed with these plants, while the better drained areas may contain a few rabbit-brush (*Chrysothamnus graveolens*) or quail-bush (*Atriplex lentiformis*). Station 13a is almost entirely covered by a pure stand of Pluchea. Cheatgrass (*Bromus rubens*) is common but not as abundant as on the upland stations. Wild mustard (*Sophia pinnata*) and foxtail (*Hordeum jubatum*) are of moderate occurrence.

TABLE 4. Perennial plants per acre on Station 13a of the Pluchea Association as calculated from quadrat counts. Numerous small semi-herbaceous *Dondia* sp. were also present.

Species	Calculated number per acre	Width in inches (Average and extremes)	Height in inches (Average and extremes)
<i>Pluchea sericea</i>	5881	33.7 (7-84)	44.8 (29-78)
<i>Chrysothamnus graveolens</i>	133	47.5 (13-116)	46.3 (18-77)
<i>Atriplex lentiformis</i>	12	36.0	45.0
Total.....	6026	34.0 (7-116)	44.8 (18-78)

The cactus-mouse (*Peromyscus e. eremicus*), Merriam kangaroo-rat (*Dipodomys merriami vulcani*), and the desert harvest-mouse (*Reithrodontomys m. megalotis*) are common mammals in the Pluchea Association. The Shivwits Plateau pocket-gopher (*Thomomys bottae nicholi*), the Sonoran white-footed mouse (*Peromyscus maniculatus sonoriensis*), and the

long-tailed pocket-mouse (*Perognathus f. formosus*) are scarce. Arizona cottontails (*Sylvilagus auduboni arizonae*) seek shelter in this association. Orr (1940: 128) reported observing this species of rabbit near the Pluchea Association in southern Nevada.



FIG. 4. Pluchea Association at Station 13a near Watercress Springs. This heavy stand of willow-like composite varies from 3 to 4 feet in height.

UPLAND ASSOCIATIONS

Larrea-Franseria Association.—This association is confined chiefly to well-drained, usually rocky, slopes of the hills and mesas of this area. The numerous low, rounded burro-bushes (*Franseria dumosa*) with their silvery foliage present a sharp contrast to the fewer, higher, bright-green creosote-bushes (*Larrea tridentata*). *Krameria* (*Krameria glandulosa*), wolfberry (*Lycium andersonii*), yellow aster (*Aster carnosus*), and various species of the cacti *Opuntia* and *Echinocereus* are common perennials. On steeper slopes, as at Station 11, *Hilaria rigida* and *Aster abatus* are numerous between rocks. Station 8 had no *Lycium* although this plant was fairly common at Station 18.

Station 8 had a greater variety of shrubs than other stations in the Larrea-Franseria Association.



FIG. 5. The lava rock hillside of the Larrea-Franseria Association at Station 11 on the Black Ridge west of Saint George, Utah.



FIG. 6. Station 18 looking northeast up the hill through the Larrea-Franseria Association. Notice the rocky nature of the surface soil.



FIG. 7. A shallow, red soil is characteristic of Station 8. The two small Larrea shrubs in the center of this picture are surrounded by smaller, light-colored Franseria.

Perennials of moderate frequency at Station 8 may be determined by reference to Table 5. The semi-shrubby *Lepidium eastwoodiae* was also of moderate frequency.

The abundant annuals are cheatgrass (*Bromus rubens*), dwarf milkvetch (*Astragalus nuttallianus trichocarpus*), and alfilaria (*Erodium cicutarium*). In the springtime, these form a dense blanket which nearly obscures the surface of the ground. Of moderate frequency are the mariposa lily (*Calochortus flexuosus*), *Plantago scariosa*, *Phacelia crenulata*, *Gilia leptomeria*, *Triodia pulchella*, *Lupinus rubens*, *Lepidium lasiocarpum*, *Eriophyllum wallacei*, *Baileya pleniradiata*, *Androstaphyllum breviflorum*, *Eriogonum inflatum*, *Eriogonum thomasi*, and *Sophia pinnata*.

The long-tailed pocket-mouse (*Perognathus f. formosus*) is abundant in this association. The common mammals are the gray rock-squirrel (*Citellus variegatus grammurus*), antelope ground-squirrel (*Citellus l. leucurus*), canyon-mouse (*Peromyscus crinitus stephensi*), and the Kaibab woodrat (*Neotoma lepida monstrabilis*). The western bat (*Pipistrellus h. hesperus*) is commonly found beneath loose rock cappings on larger boulders and in crevices where it apparently spends daytime hours during most of the year. Cantwell's bat (*Antrozous pallidus cantwelli*) is also occasionally found in such situations.

Of moderate frequency in this association are the Nevada ring-tailed cat (*Bassariscus astutus nevadensis*), Great Basin spotted skunk (*Spilogale gracilis saxatilis*), Colorado Desert jackrabbit (*Lepus californicus deserticola*), cactus-mouse (*Peromyscus e. eremicus*), house mouse (*Mus musculus*), and Merriam kangaroo-rat (*Dipodomys merriami vulcani*), specimens of which have been taken. The Mexican free-tailed bat (*Tadarida mexicana*) is also known from fissures in rocks and ledges of this association.

The desert kit fox (*Vulpes macrotis arsipus*),

TABLE 5. Perennial plants per acre on stations in the Larrea-Franseria Association as calculated from quadrat counts.

Species	Stations	Calculated number per acre			Width in inches (Average and extremes)			Height in inches (Average and extremes)		
		8	11	18	8	11	18	8	11	18
<i>Larrea tridentata</i>	157	121	375	45.9(13-96)	53.2(21-66)	41.9(9-82)	36.9(11-60)	49.1(23-58)	37.5(13-66)	
<i>Franseria dumosa</i>	2360	2287	569	17.9(2-39)	27.6(5-59)	27.1(12-42)	11.9(2-21)	15.5(5-27)	16.4(10-28)	
<i>Krameria glandulosa</i>	157	73	254	29.9(14-45)	35.0(20-49)	28.6(8-46)	13.2(8-18)	18.0(14-25)	15.6(7-23)	
<i>Lycium andersonii</i>	0	61	278	41.6(34-47)	41.6(34-47)	37.6(11-60)	28.2(14-34)	24.6(9-34)		
<i>Opuntia</i> sp.....	48	12	12	12.0(10-15)	12.0	15.0	11.0(10-13)	14.0	12.0	
<i>Aster carnosus</i>	24	85	0	14.5(8-21)	18.6(13-29)		14.0(11-17)	15.6(6-21)		
<i>Aster abatus</i>	0	2033	0	15.1(8-27)	15.1(8-27)		19.1(14-26)			
<i>Hilaria rigida</i>	0	1174	0	22.5(12-46)	22.5(12-46)		23.1(17-28)			
<i>Grayia spinosa</i>	12	0	12	14.0		37.0	11.0		25.0	
<i>Atriplex confertifolia</i>	157	0	0	19.9(9-39)			14.9(8-27)			
<i>Parosela johnsoni</i>	97	0	0	43.8(22-58)			21.5(13-27)			
<i>Coleogyne ramosissima</i>	48	0	0	21.5(8-31)			19.3(13-24)			
<i>Gutierrezia lucida</i>	48	0	0	26.0(2-38)			19.4(31-28)			
<i>Encelia frutescens</i>										
<i>virginensis</i>	36	0	0	12.8(21-24)			10.3(3-20)			
<i>Tetradymia azillaris</i>	12	0	0	52.0			38.0			
<i>Atriplex canescens</i>	12	0	0	15.0			10.0			
Total.....	3168	5844	1500	20.9(2-96)	22.8(5-66)	33.0(8-82)	13.9(2-60)	19.1(5-58)	23.1(7-66)	

TABLE 6. Perennial plants per acre on stations in the Larrea Association as calculated from quadrat counts.

Species	Stations..	Calculated number per acre			Width in inches (Average and extremes)			Height in inches (Average and extremes)		
		10	12	16	10	12	16	10	12	16
<i>Larrea tridentata</i>		109	73	750	41.2(8-63)	24.5(17-43)	35.7(5-190)	38.0(9-53)	24.2(11-55)	30.9(5-88)
<i>Ephedra nevadensis</i>		351	1198	12	26.7(14-46)	24.6(1-57)	14.0	19.3(12-27)	19.3(6-29)	12.0
<i>Lycium andersonii</i>		387	218	230	34.5(9-63)	18.2(3-40)	21.0(7-38)	23.0(10-35)	15.8(6-24)	19.2(9-35)
<i>Krameria glandulosa</i>		169	206	0	32.7(14-42)	32.7(13-45)	15.7(8-21)	15.6(12-19)
<i>Aster carnosus</i>		12	24	0	20.0	17.0(14-20)	16.0	14.5(14-15)
<i>Grayia spinosa</i>		12	12	0	33.0	15.0	23.0	12.0
<i>Franseria dumosa</i>		0	496	0	22.1(2-39)	16.9(3-25)
<i>Opuntia</i> sp. and <i>Echinocereus</i> sp.		0	48	24	10.0(8-12)	13.0(11-15)	12.8(11-14)	10.0(10-10)
<i>Hymenoclea salsola</i>		0	0	12	27.0	20.0
Total.....		1040	2275	1028	32.1(8-63)	23.7(1-57)	31.5(5-190)	22.0(8-53)	18.1(3-55)	27.4(5-88)

desert coyote (*Canis latrans estor*), gray fox (*Urocyon cinereoargenteus scotti*), and desert bobcat (*Lynx rufus baileyi*) have been taken by trappers in this area, the latter three being seen infrequently.

Larrea Association.—This association is found on nearly level areas where drainage is good and the salt content of the soil is low. It is characterized by a good stand of creosote-bush which not infrequently may be from three to seven feet in height. Occasionally, as at Station 12 (Table 6), there may be a few burro-bushes in the stonier areas, but these plants are more frequently replaced by the common Nevada jointfir (*Ephedra nevadensis*). These rockier flats, where the creosote-bush tends to be smaller, may also commonly support *Krameria*, *Lycium*, and *Lepidium eastwoodiae*. Stations 10 and 16 have small amounts of *Hymenoclea salsola*, *Opuntia* and *Echinocereus*. *Baileya pleniradiata* and *Grayia spinosa* are scarce at Station 12.

The abundant annuals which blanket the spaces between the perennials during the early spring months are cheatgrass (*Bromus rubens*), *Astragalus nuttallianus trichocarpus*, *Erodium cicutarium*, and *Eriogonum inflatum*. Common are the mariposa lily (*Calochortus flexuosus*), *Plantago scariosa*, *Sphaeralcea ambigua*, *Delphinium amabile*, *Baileya pleniradiata*, *Sphaeralcea munroana*, *Allionia incarnata*, *Chaenactis macrantha*, *Lepidium perfoliatum*, *Lupinus rubens*, and poverty grass (*Aristida purpurea*).



FIG. 8. The Larrea Association on Harrisburg stony loam at Station 10. The Pine Valley Mountains (summit 10,300 ft.) can be seen about 22 miles to the north-east.



FIG. 9. Widely spaced creosote-bushes at Station 16 in the Larrea Association.



FIG. 10. Looking westward to the Beaverdam Mountains from the top of the Black Ridge at Station 12. Notice the "desert pavement," the *Ephedra* (foreground), and the *Larrea* (dark in color in the background).

The mammals common in the Larrea Association are the antelope ground-squirrel (*Citellus l. leucurus*), Virgin Valley pocket-mouse (*Perognathus longimembris virginis*), Merriam kangaroo-rat (*Dipodomys merriami vulcani*), Colorado Desert jackrabbit (*Lepus californicus deserticola*), and the Arizona cottontail (*Sylvilagus auduboni arizonae*). Of moderate frequency are the long-tailed pocket-mouse (*Perognathus f. formosus*), the desert coyote (*Canis latrans estor*), Virgin Valley kangaroo-rat (*Dipodomys microps celsus*), Stephens canyon-mouse (*Peromyscus crinitus stephensi*), and the Kaibab woodrat (*Neotoma lepida monstabilis*).

Clistoyucca-Larrea Association.—This association is west of the Beaverdam Mountains. Station 9 supports a great variety of plant life, the most noticeable floral feature being the widely-spaced Joshua trees (*Clistoyucca brevifolia*) which may reach a height of fifteen feet. The creosote-bushes, also widely spaced, are rather uniformly distributed over the area. Rather irregularly or patchily distributed are the common shrubs: *Lycium andersonii*, *Franseria dumosa*, *Eurotia lanata*, *Ephedra nevadensis*, and *Krameria glandulosa*. A number of species of *Echinocereus* and *Opuntia*, including arborescent types of the latter, also occur. Usually growing in the shelter of a shrub, are clumps of *Hilaria rigida* and *Muhlenbergia porteri*, common grasses of the area. Colonies of *Yucca baccata*, moderate in number, are irregularly distributed.

Perennial shrubs moderate in number include *Salazaria mexicana*, *Thamnosma montana*, *Ephedra torreyana*, *Encelia frutescens virginensis*, *Psilostrophe cooperi*, *Salvia carnosa*, *Tetradymia axillaris*, *Hymenoclea salsola*, and *Gutierrezia lucida*.

TABLE 7. Perennial plants per acre on Station 9 in the Clistoyucca-Larrea Association as calculated from quadrat counts.

Species	Calculated number per acre	Width in inches (Average and extremes)	Height in inches (Average and extremes)
<i>Clistoyucca brevifolia</i> . . .	48	104.8(87-137)	125.5(99-169)
<i>Larrea tridentata</i>	218	41.8(22- 79)	28.2(12- 46)
<i>Franseria dumosa</i>	823	19.1(5- 35)	11.8(5- 20)
<i>Eurotia lanata</i>	545	11.8(5- 23)	12.3(6- 25)
<i>Lycium andersonii</i>	206	25.5(4- 46)	15.2(6- 27)
<i>Ephedra nevadensis</i>	254	17.9(6- 38)	12.1(6- 18)
<i>Salazaria mexicana</i>	48	33.8(26- 38)	25.8(21- 33)
<i>Aster carnosus</i>	36	12.3(7- 17)	10.7(8- 14)
<i>Opuntia echinocarpa</i>	24	7.5(7- 8)	15.5(10- 21)
<i>Opuntia</i> sp.	12	10.0	11.0
<i>Encelia frutescens virginensis</i>	12	16.0	10.0
Total	2226	28.3(4-137)	21.5(5-169)

The abundant springtime blooming annuals include the dwarf milkvetch (*Astragalus nuttallianus trichocarpus*), cheatgrass (*Bromus rubens*), *Plantago scariosa*, and alfalfa (*Erodium cicutarium*). Moderate in number are *Welwitschia floccosa*, *Eriogonum inflatum*, *Gilia leptomeria*, *Ptiloria exigua*, *Eriogonum deflexum*, *Calochortus flexuosus*, and *Delphinium amabile*.

Common mammals include the Arizona cottontail (*Sylvilagus auduboni arizonae*), Colorado Desert jackrabbit (*Lepus californicus deserticola*), Woodbury kangaroo-rat (*Dipodomys microps woodburyi*), and Merriam kangaroo-rat (*Dipodomys merriami merriami*). The Mohave pocket-mouse (*Perognathus formosus mohavensis*), desert woodrat (*Neotoma l. lepida*), desert bobcat, desert coyote, Great Basin spotted skunk, antelope ground-squirrel, cactus-mouse, and long-tailed scorpion-mouse (*Onychomys torridus longicaudus*) are of moderate frequency in this association.



FIG. 11. Clistoyucca-Larrea Association at Station 9 on the Beaverdam Slope. The rocky Beaverdam Mountains can be seen in the east.

Emplectocladus Association.—This association is found along dry washes which bisect the Clistoyucca Association. The California desert-almond (*Emplectocladus fasciculatus*) is a large, rounded, dark-green shrub which usually reaches a height of four or five feet and has a diameter of from six to ten feet. With the exception of a greater number of *Salazaria mexicana* shrubs, the other plants found in these gravelly washes are mostly those characteristic of the surrounding Clistoyucca Association. No attempt was made to measure or study thoroughly the plants and animals of this association, although some trapping was done.

Common mammals include the antelope ground-squirrel, cactus-mouse, Stephens canyon-mouse, Mohave long-tailed pocket-mouse (*Perognathus formosus mohavensis*), and the desert woodrat (*Neotoma l. lepida*). The desert bobcat, desert coyote, and the Great Basin spotted skunk are known to seek homes here.

Coleogyne Association.—This association is common on areas where the extremely shallow soils cover layers of rock, usually sandstone, such as at Station 13c. These plants are able to grow in cracks in the rock or upon the shallow soil above the rocky layer. Small matchweed (*Gutierrezia lucida*), blackbrush (*Coleogyne ramosissima*), and *Hymenoclea salsola* are common perennials while *Bromus rubens*, *Astragalus n. trichocarpus*, and *Erodium cicutarium* are abun-



FIG. 12. Typical Joshua trees (*Clistoyucca brevifolia*) at Station 9 on the Beaverdam Slope of Washington County, Utah.

dant annuals. Other springtime plants of moderate frequency are *Baileya pleniradiata*, *Tridodium pulchella*, *Eriophyllum wallacei*, *Eriophyllum lanosum*, *Lepidium lasiocarpum*, *Calochortus flexuosus*, *Gilia leptomeria*, *Plantago scariosa*, and *Sphaeralcea ambigua*. The small, yellow-blossoming *Pectis papposa* is common in late summer and early autumn. *Lepidium eastwoodiae* is found in patches in some parts of this association.

TABLE 8. Perennial plants per acre on Station 13c in the Coleogyne Association as calculated from quadrat counts.

Species	Calculated number per acre	Width in inches (Average and extremes)	Height in inches (Average and extremes)
<i>Gutierrezia lucida</i>	3243	10.5(2-36)	10.5(2-24)
<i>Hymenoclea salsola</i>	290	28.4(15-42)	17.1(12-22)
<i>Coleogyne ramosissima</i>	242	14.5(6-40)	10.1(5-17)
<i>Larrea tridentata</i>	24	92.0(78-106)	49.0(48-50)
<i>Krameria glandulosa</i>	12	42.0	19.0
<i>Prosopis glandulosa</i>	12	50.0	25.0
<i>Lycium andersonii</i>	12	16.0	17.0
<i>Atriplex confertifolia</i>	12	17.0	17.0
Total.....	3847	12.8(2-106)	11.5(2-50)



FIG. 13. Coleogyne Association at Station 13c near Saint George. Notice the sandstone showing through the extremely shallow soil in the lower left corner of the picture and the numerous *Gutierrezia* plants anchored in the cracks of the rock.

The mammal most common in this association is the long-tailed pocket-mouse (*Perognathus f. formosus*), which probably finds shelter beneath scattered rocks. The Kaibab woodrat (*Neotoma lepida monstrabilis*) and Stephens canyon-mouse (*Peromyscus crinitus stephensi*) are of moderate occurrence. The cactus-mouse (*Peromyscus e. eremicus*) is scarce.

Atriplex-Hilaria Association.—This association usually exists on residual soils of terraces or similar, not too shallow, slightly salty, soils. The large, gray, four-wing saltbushes (*Atriplex canescens*) are usually widely spaced, the intervening areas being partially occupied by clumps of grass (*Hilaria rigida*). The bases of the few spiny *Lycium andersonii* bushes seem to be favored as digging places by the kangaroo-rat (*Dipodomys microps celsus*). Numerous short clumps of winter fat (*Eurotia lanata*) add to the uniform grayness of the floral aspect. Most of the *Opuntia* found here, although few in number, are of

the arborescent type commonly called cholla (*Opuntia echinocarpa*). Station 7 very well represents this association.



FIG. 14. A kangaroo-rat mound (*Dipodomys microps celsus*) in the buffy-colored soil beneath a *Lycium* shrub at Station 7 south of Saint George, Utah. The Beaverdam Mountains on the western horizon are about 18 miles distant.

Because galleta grass (*Hilaria rigida*) furnishes good food for livestock, the areas covered by this association are frequently overgrazed. In spite of this, the following abundant annuals survive: *Bromus rubens*, *Baileya pleniradiata*, *Erodium cicutarium*, and *Eriogonum inflatum*. Blackeyed Susan (*Gaillardia gracilis*), *Aster canescens*, and *Astragalus nuttallianus trichocarpus* are scarce.

TABLE 9. Perennial plants per acre on Station 7 in the Atriplex-Hilaria Association as calculated from quadrat counts.

Species	Calculated number per acre	Width in inches (Average and extremes)	Height in inches (Average and extremes)
<i>Atriplex canescens</i>	363	20.6(6-47)	14.2(6-35)
<i>Hilaria rigida</i>	1283	15.2(6-42)	10.5(5-28)
<i>Eurotia lanata</i>	436	11.2(4-23)	13.0(6-21)
<i>Opuntia echinocarpa</i>	36	16.3(4-31)	17.0(6-29)
<i>Lycium andersonii</i>	24	60.0(30-90)	35.5(24-47)
Total.....	2142	15.9(4-90)	12.0(5-47)

Common mammals are the kangaroo-rats: *Dipodomys microps celsus* and *D. merriami vulcani*. More long-tailed scorpion-mice (*Onychomys torridus longicaudus*) were taken in this association than in any other habitat. In the slightly more rocky areas, especially along small ravines, *Perognathus f. formosus* is common. The Colorado Desert jackrabbit and antelope ground-squirrel are moderate in number. The Sonoran white-footed mouse (*Peromyscus maniculatus sonoriensis*), Stephens canyon-mouse (*Peromyscus crinitus stephensi*), Arizona cotton-tail, Kaibab woodrat (*Neotoma lepida monstrabilis*), and Shivwits Plateau pocket-gopher (*Thomomys bottae nicholi*) are scarce in this association.

Atriplex confertifolia Association.—This association is usually confined to flats which are too salty to support other types of plant life, such as at Sta-

TABLE 10. Perennial plants per acre on stations in the *Atriplex confertifolia* Association as calculated from quadrat counts.

Species	Station..	Calculated number per acre		Width in inches (Average and extremes)		Height in inches (Average and extremes)	
		14a	14b	14a	14b	14a	14b
<i>Atriplex confertifolia</i>		1755	1065	22.4(5-40)	25.5(5-54)	15.5(3-28)	17.5(6-27)
<i>Lycium andersonii</i>		12	157	40.0	42.8(18-72)	30.0	26.1(17-35)
<i>Hymenoclea salsola</i>		0	2081		25.8(7-46)		20.1(9-29)
<i>Dondia</i> sp.....		2396	0	14.9(5-33)		8.2(3-24)	
<i>Gutierrezia lucida</i>		0	254		16.4(5-42)		15.3(9-28)
<i>Opuntia</i> sp.....		24	0	21.0(21-21)		15.0(14-16)	
<i>Parosela johnsonii</i>		0	157		39.5(20-60)		23.9(16-32)
<i>Aster carnosus</i>		0	97		13.6(9-21)		15.0(12-23)
<i>Tetradymia axillaris</i>		0	97		43.0(23-67)		31.3(27-37)
<i>Atriplex canescens</i>		0	24		38.0(34-42)		30.5(28-33)
Total.....		4187	3932	18.2(5-40)	26.0(5-72)	11.3(3-30)	19.7(6-37)

tion 14a. The dominant plant is the low, rounded, widely-spaced shadscale (*Atriplex confertifolia*). The interspaces are sometimes partially filled with *Dondia* sp., especially in areas with poor drainage. In some parts of this association, the soils which are on slight ridges and are better drained, as at Station 14b, support a greater variety of plant life than is found on the lower areas.

A very few *Opuntia* of the prickly pear type and an occasional *Lycium* are found mixed with the shadscale. Some *Lepidium eastwoodiae* is also present, but in reduced size and numbers of plants.

On the saline flats, between the shadscale plants, *Bromus rubens*, *Eriogonum inflatum*, *Phacelia pulchella*, and *Phacelia fremonti* are abundant after the winter rains. Mosses and lichens often form a dry crust over the surface of the soil and become active only during wet seasons. Common annuals include *Erodium cicutarium* and *Mimulus parryi*. Moderate in number are *Mentzelia pumila*, *Chaenactis macrantha*, *Cryptanthus nevadensis*, *Chlysmia tenuissima*, *Baileya pleniradiata*, *Triodia pulchella*, *Astragalus nuttallianus trichocarpus*, *Eriogonum deflexum*, *Sphaer-*

rostigma decorticans, *Cryptanthus pterocarya*, and *Lygodesmia exigua*.

On the sandy ridges, the abundant plant mixed with the shadscale is *Hymenoclea salsola*. *Lycium andersonii*, *Lepidium eastwoodiae*, *Parosela johnsonii*, *Tetradymia axillaris*, *Aster carnosus*, and *Gutierrezia lucida* are common. Indian rice grass (*Oryzopsis hymenoides*) and galleta (*Hilaria rigida*) are common perennial grasses. Station 14b represents an extreme case showing more *Hymenoclea* plants than *Atriplex*. However, as viewed from the surrounding flats, the area as a whole is covered by *Atriplex confertifolia* and it is not thought desirable to recognize a separate *Hymenoclea* Association at this time.

The abundant annuals on these *Hymenoclea* ridges are *Bromus rubens*, *Eriogonum inflatum*, and *Hordeum jubatum*. Common are *Ptiloria exigua pentachaeta*, *Chaenactis macrantha*, *Aster canescens*, *Gilia polycladon*, *Gilia leptomeria*, *Welwitschia floccosa*, *Phacelia pulchella*, *Cryptanthus pterocarya*, *Sphaerostigma decorticans*, and *Mimulus parryi*.

There seems to be no significant difference in varieties of mammals present in each of these two phases of the *Atriplex confertifolia* Association. Common are the kangaroo-rat (*Dipodomys microps celsus*), Virgin Valley pocket-mouse (*Perognathus longimembris virginis*), and the antelope ground-squirrel (*Citellus l. leucurus*). There is also one record of the cactus-mouse (*Peromyscus e. eremicus*) and one of the Merriam kangaroo-rat (*Dipodomys merriami vulcani*).

Prosopis Association.—This association is found on deep, usually loose soils where there is likely to be a fair amount of soil water present. The large mesquite bushes (*Prosopis glandulosa*) may reach a height of about twelve feet and spread to a diameter of twenty-five feet, when not crowded. These plants may be few and widely spaced or rather dense as at Station 17. Occasionally, the gray-white foliage of a few sand-sagebrush (*Artemisia filifolia*) produces a marked contrast to the dark green of the mesquite, of the less common rabbitbrush (*Chrysothamnus*



FIG. 15. *Hymenoclea* bushes (foreground) on sandy soils with *Atriplex confertifolia* in the distance. The Black Ridge as seen from the west at Stations 14a and 14b.

graveolens), and of *Hymenoclea fasciculata*. However, the sand-sagebrush is usually present only where the soils are somewhat loose and sandy.



FIG. 16. A mesquite (*Prosopis glandulosa*) at Station 17.

The abundant annuals at Station 17 are *Bromus rubens* and *Baileya pleniradiata*. Common or of moderate occurrence are tobacco (*Nicotiana attenuata*), Russian thistle (*Salsola pestifer*), Rocky Mountain Bee plant (*Cleome lutea*), foxtail (*Hordeum jubatum*), *Sophia pinnata*, *Datura meteloides*, *Erodium cicutarium*, and *Gilia gymnoclada*.

TABLE 11. Perennial plants per acre on Station 17 in the Prosopis Association as calculated from quadrat counts.

Species	Calculated number per acre	Width in inches (Average and extremes)	Height in inches (Average and extremes)
<i>Prosopis glandulosa</i>	145	168.3(32-284)	98.7(29-138)
<i>Artemisia filifolia</i>	823	18.4(3- 87)	19.8(7- 53)
<i>Chrysothamnus graveolens</i>	254	77.8(17-156)	51.2(27- 79)
<i>Larrea tridentata</i>	24	125.0(89-161)	92.0(91- 93)
Total	1246	50.1(3-284)	36.8(7-138)

Merriam kangaroo-rat (*Dipodomys merriami vulcani*) is common in this association. The desert harvest-mouse (*Reithrodontomys m. megalotis*) and the Shivwits Plateau pocket-gopher (*Thomomys bottae nicholi*) have also been taken. The Arizona cotton-tail has been frequently observed.

Artemisia filifolia Association.—This association is common in the Saint George Basin wherever loose, recently-formed, sands occur. On these areas the sand-sagebrush is abundant. Occasionally a few *Prosopis glandulosa* may be present as at Station 15, but this is not always so in the region studied. *Hymenoclea* is common in this association.

The abundant annuals are *Bromus rubens*, *Baileya pleniradiata*, *Gilia gymnoclada*, *Erodium cicutarium*, and *Triodia pulchella*. Of less abundance are *Ptiloria exigua pentachaeta*, *Eriophyllum wallacei*, *Cryptantha pterocarya*, and *Sophia pinnata*.

The Merriam kangaroo-rat (*Dipodomys merriami vulcani*) is abundant at Station 15 in the *Artemisia filifolia* Association. Mammals that are scarce in-



FIG. 17. *Artemisia filifolia* Association in the coarse sands of Station 15. *Prosopis* can be seen in the distance.

clude the Virgin Valley pocket-mouse (*Perognathus longimembris virginis*), the long-tailed scorpion-mouse (*Onychomys torridus longicaudus*), the Kaibab wood-rat (*Neotoma lepida monstrabilis*), the desert harvest-mouse (*Reithrodontomys m. megalotis*), and the Shivwits Plateau pocket-gopher (*Thomomys bottae nicholi*).

TABLE 12. Perennial plants per acre on Station 15 in the *Artemisia filifolia* Association as calculated from quadrat counts.

Species	Calculated number per acre	Width in inches (Average and extremes)	Height in inches (Average and extremes)
<i>Artemisia filifolia</i>	1537	30.9(2- 89)	24.8(4-52)
<i>Prosopis glandulosa</i>	12	310.0	130.0
<i>Larrea tridentata</i>	24	106.0(99-113)	72.5(72-73)
<i>Hymenoclea fasciculata</i>	61	14.6(2- 55)	9.8(4-22)
Total	1634	33.4(2-113)	25.7(4-73)

Chrysothamnus Association.—This association is represented at Station 13b. In addition to rabbit-brush (*Chrysothamnus graveolens*), the noticeable perennials include *Atriplex lentiformis*, *Larrea tridentata*, and *Dondia* sp. These species, except for *Dondia*, are somewhat bunched in their arrangement, leaving the intervening spaces bare when not covered in the spring by such abundant annuals as *Bromus rubens*, *Erodium cicutarium*, *Baileya pleniradiata*, and *Sophia pinnata*. Plants that are scarce include *Lepidium eastwoodiae* and *Nicotiana attenuata*.

TABLE 13. Perennial plants per acre on Station 13b in the *Chrysothamnus* Association as calculated from quadrat counts.

Species	Calculated number per acre	Width in inches (Average and extremes)	Height in inches (Average and extremes)
<i>Chrysothamnus graveolens</i>	823	50.6(12-113)	43.4(18-72)
<i>Dondia</i> sp.	629	8.8(3- 48)	7.6(4-37)
<i>Larrea tridentata</i>	169	68.8(58- 91)	43.4(18-72)
<i>Atriplex lentiformis</i>	103	19.5(4- 60)	23.7(6-55)
<i>Artemisia filifolia</i>	73	40.2(11- 64)	29.0(13-51)
Total	1801	35.4(4-113)	32.1(4-69)



FIG. 18. Chrysothamnus Association on the red sandstone soils of Station 13b near Watercress Springs in the Saint George, Utah, area. Southeast is an arch, a forerunner of a natural bridge.

Mammals were very scarce at Station 13b, this being the least populated field station. There are records of the Merriam kangaroo-rat (*Dipodomys merriami vulcani*), long-tailed pocket-mouse (*Perognathus f. formosus*), cactus-mouse (*Peromyscus e. eremicus*), and the Shivwits Plateau pocket-gopher (*Thomomys bottae nicholi*).

FACTORS THAT INFLUENCE THE LOCAL DISTRIBUTION OF THE PLANTS

CLIMATES

The macroclimate should be about the same over all of the area studied since all of the stations are located close together within the same general region and all are in the same life belt of the Mohavian Biotic Province. Alter (1931:21-2) states that in southern Utah, the average annual temperature falls about one degree Fahrenheit for each rise of about 225 feet in altitude. However, the average annual temperature at Springdale in the Virgin Valley, which is one thousand feet higher in elevation, is not significantly different from that at Saint George. Also, since the greatest variation in altitude between any of the stations is but little more than 600 feet, the macroclimate must be similar over the area studied. With the exception of Station 9, these collecting areas are within a three mile radius of Saint George, hence the rainfall should not vary greatly. The differences in macroclimate between these stations is, then, likely very small.

The various microclimates will differ, but, in the area studied, these differences were not enough to confine any one association to any given exposure. The microclimates themselves will be different principally because of different soil conditions. As mentioned previously, Shreve (1925:103) states that the local distribution of plants in the California deserts is "chiefly determined by the small differences in moisture conditions, such as are maintained by site,

shading, or texture of the soil." These factors are discussed separately insofar as the data obtained will permit.

BARRIERS

Because of the rough, broken topography in the Saint George region, certain physiographic features probably act as barriers to living organisms. One of the more obvious barriers is the Beaverdam Mountain Range. This probably forms a barrier to mammals because the extremely rocky type of soil of these mountains differs from that of the alluvial fans to the west and from that of the sandstones to the east. Then too, these mountains form a north and south barrier which cuts off the otherwise completely enclosed Saint George Basin from the low-lying desert areas to the southwest. These mountains are cut by the Virgin River which passes through a narrow, very rocky gorge known as the Virgin Narrows.

The importance of this Beaverdam Mountain Range as a dividing line between the Colorado Plateau and the Basin-and-Range physiographic provinces has been pointed out by Gardner (1941:245). The mountain range is also a separating line from a biological standpoint. The Joshua tree (*Clistoyucca brevifolia*) is found on the west side of these mountains and has entered the Motoqua Pass and nearly reached the drainage system of Santa Clara Creek near Jackson Spring. This plant is also found in a rather limited area on the east slope of the Beaverdam Mountains along the old Wells-Fargo Express road where it enters the pass south of the Apex mine. These trees seem to be near this mountain pass as if they had but rather recently entered this basin. Many nearby hillsides with similar favorable conditions have not as yet been invaded.

Joshua trees thrive and bloom when transplanted to areas on the east side of the Beaverdam Mountains where they do not naturally occur. They have done so in the cactus garden of the Dixie Junior College at Saint George for a number of years. Altitudes and soils similar to those of the Beaverdam Slope are present in the Saint George Basin, so that if the Joshua tree were once established in the latter area, it should survive.

The Saint George Basin represents the middle part of the large block west of the Hurricane Fault which has dropped from 1,500 to 10,000 feet. This was "after large parts of the Basin-and-Range province had received thick Tertiary and Quaternary deposits" (Gardner 1941:244). Since this comparatively recent lowering of the Saint George area, some forms of life (such as the plants *Larrea* and *Franeria*, and animals to be listed later) have been able to cross these mountains into the Saint George Basin while the Joshua tree and some other forms have not yet completed their invasion.

SOIL WATER

Plants are important as indicators of soil moisture as has been shown by Clements (1920:76); Shantz (1938:850) and other workers. Although the rainfall difference between any two stations may be negligible,

there will be at most times a difference between them in the amount of their soil moisture. This is true because the chemical makeup, the depth and texture of the soil as well as the presence or absence of a hardpan and the degree of slope influences the amount of soil moisture present.

No attempt was made to measure quantitatively the amount of soil water actually present at any station. Shantz (1938:851) states that in deep soil, the mesquite is an indicator of available water. This, together with the fact that a small but permanent stream of water was in the fourteen foot deep wash near Station 17 seems to indicate that soil moisture was an important factor supporting the heavy growth of *Prosopis* at that place. *Pluchea* is a plant of the riparian associations and probably available soil moisture was responsible in part for its abundance at Station 13a, located near this same wash but farther upstream, where it was more shallow. Since the soil at Station 15 was of fine sandy loam upon a deep sandstone layer, accumulated soil moisture may also have accounted for the heavy growth of *Artemisia* and the few *Prosopis* there.

Dondia is an indicator of moisture in saline soils according to Shantz (1938:852). This plant occurs at Stations 13a, 13b, and 14a, although at the latter place it was scanty in growth. The available soil water in the shallow soil at Station 14a undoubtedly did not remain in quantities very long, for the soil down to the hardpan was usually quite dry and dusty except shortly after heavy rains. If one were to judge by the plant cover and the topographical location, the remaining stations did not have as much available soil moisture as those listed.

SOIL DEPTH

A hard substratum of some sort was present at those stations with the most soil water. Indeed, various kinds of hard layers exist at different depths at most or all stations. A "caliche," or limestone hardpan, was present at Stations 10, 12, and 16; a gypsum-limestone layer existed at 14a and 14b; a layer of sandstone lay beneath the soils at Stations 8, 11, 13a, 13b, 13c, 15, and 17; a gravel-limestone combination was at 9, while the ultimate hard layer beneath Stations 7 and 18 is unknown, but is assumed to be sandstone.

Stations with the greatest supply of soil water are usually those with a sandstone layer more than six or eight feet below the surface and located near a watercourse, judging from the foregoing data. Probably a lesser amount of soil moisture existed in the topsoils with a hardpan near the surface as at Station 14a.

Extremely shallow soils, such as exist at Station 13c (Table 2), may be presumed to hold soil water for only a very short time. This field station is occupied by a good stand of *Gutierrezia* and *Coleogyne* and there is but little *Larrea*. The soil is washed away almost as rapidly as it is formed, hence these plants, which are able to grow in rock fissures or upon the thin soil cover, can be expected to be dominant here for some time.

In shallow soils (Table 2) deeper than those at Station 13c, some *Larrea* and much *Franseria* grew, when this condition occurred on steep slopes. However, this same association was found on the deeper clay soil of Station 18. At Station 14a where mineral salts were concentrated in the shallow soil, *Atriplex confertifolia* was common. The desert beauty (*Parosela johnsoni*) and *Hymenoclea salsola* seemed to favor shallow soils with small amounts of mineral salts (as at Stations 8 and 14b).

In soils of medium depth, as at Station 16, the *Larrea* was large and abundant. The soils at Stations 10 and 12 were more shallow than at 16 and the growth of creosote-bush was not as heavy as at this latter place. This agrees with the statement of Shantz (1938:851) that a stony, shallow soil is indicated by poor growth of creosote-bush.

Soils deeper than four feet were usually sandy and were covered by *Pluchea*, *Artemisia*, *Prosopis*, or *Atriplex canescens*. However, *Prosopis* did occur on hillsides or rocky situations, though in such places it usually was dwarfed.

CHEMICAL COMPOSITION OF SOIL

The carbonates which were present in the soil at most of these field stations in both the water soluble and in the insoluble form, seem to have less direct effect upon the plant life than do the chlorides and sulphates, since most of the plants are probably able to tolerate these moderate concentrations of soluble carbonates. The most important effect of limestone in the soil probably is the frequent formation of a "caliche" or hardpan, such as that at Stations 10, 12, and 16 in the *Larrea* Association. Shreve and Mallery (1933:112) state that "the chemical properties of highly calcareous soils appear to be of less importance than the physical in relation to the growth of *Larrea*." Mallery (1935:33) found that the presence of "caliche" in close proximity to the root system does not effect the absorption of calcium by creosote-bush. In some cases he found that the creosote-bushes were benefited where they were able to penetrate the caliche and draw upon the water stored beneath this hardpan.

Soils without large amounts of lime support the *Prosopis*, the *Artemisia*, or the *Coleogyne* Associations (Tables 3, 8, 11, and 12). However, the data do not show whether the lack of lime or the sandy texture of the soil is the more important factor, although it is thought to be the latter.

Sodium sulphate seems to be a common and harmful "alkali" as may be seen in Table 3. Sodium chloride occurs in most, but not all, places where the sulphate is found. The chloride occurs in lesser concentration than the sulphate and in such areas probably increases the salt concentration with which plant roots must contend.

Various plants, such as *Atriplex confertifolia* and *Pluchea sericea*, are known as indicators of mineral salts. These plants, then, are limited in their distribution by these salts only when in the greatest concentrations, such as at the edge of Station 13a (5.82% sodium chloride and 24.56% sodium sulphate)

where no plants were growing. *Eurotia lanata* (Stations 7 and 9), *Atriplex canescens* (Station 7), and *Parosela johnsoni* are examples of plants which were found where there is a small amount of sodium sulphate, usually in the subsoil. Judging from their distribution, *Artemisia*, *Prosopis*, *Larrea*, and *Franseria* are plants less tolerant of "alkali."

GRADIENT

The steeper slopes usually have soils of a coarser texture than the more nearly level areas (Table 1). With stony soils, topsoil particles of granule gravel vary in amount according to the gradient, if the parent materials are at all similar. Stations 9 and 13c, the first named with small rocks and the last-named entirely lacking in rocks, are not comparable with others which are located upon slopes, for these were on alluvial deposits where the soil was not being weathered directly from the parent material.

Station 9 is on a broad alluvial fan where conglomerate gravel and limestones washed from the Beaverdam Mountains caused the amount of fine gravel to be greater than otherwise would have been expected on the basis of the gradient. At Station 13a, the soil was Saint George fine sand which had been deposited by water from nearby fine red sandstone. The intermittent flow of water from small "seeps" as well as from thundershowers, has scoured out a secondary channel to bedrock leaving vertical sandy sides. No fine gravel was found in this sand.

The "alkalis" are less likely to occur upon steep slopes, probably because drainage there is good and the water removes soluble material as rapidly as it is dissolved from the parent material. The fine particles of soil also are promptly removed from steep slopes leaving coarse particles which are probably less likely to hold soluble mineral salts. The clay in the gravelly, light clay loam at Station 18 contained more sodium sulphate and sodium chloride than the soils of other stations which had coarser soils and were located upon steep slopes. The surface crust which forms when the ground dries after a rainstorm is usually neither as hard nor as thick upon the soils of steep slopes as upon low-lying, finer soils.

Stations upon steep slopes, when compared with those of more nearly level areas, are usually more stony or gravelly because of rapid washing away of the finer soil particles, hence they are drier and less saline than are the low-lying stations. "Alkali" tolerant plants such as *Atriplex confertifolia*, *Pluchea sericea*, and *Dondia* sp. will usually be found upon more nearly level areas, while the slopes are more likely to support *Franseria*, *Gutierrezia*, and *Coleogyne*.

SLOPE EXPOSURE

Differences in the direction of exposure to sun and to wind of the stations here described, produced no appreciable difference in plant cover. The plants are frequently the same on northern as on southern exposures, probably because all stations were near one another and, at this altitude where snow does not remain on north slopes during the winter, are sub-

jected to the same long, intense dry period. Hillsides facing north seemed eventually to become about as hot and dry as hillsides facing south or west. South-facing hillsides and north-facing hillsides would likely have shown temperature differences, but these variations were within the limits of the range of temperature toleration of the various plant associations in this life belt. The *Larrea-Franseria* Association, for example, may be found on a slope exposure facing north, south, east, or west at this altitude. Had the area been nearer the upper limit of the Lower Sonoran Life Belt, it is likely that the influence of slope exposure would have been more noticeable.

SOIL TEXTURE

The texture of the soil is influenced by the location and slope of the area, by the presence or absence of water, and by the parent materials and their physical and chemical composition. Since the plant cover is comparatively scanty in the area, the direct action of plants in soil fragmentation, although present and important, will not differ greatly between any two stations. The same may be said about animals and their digging activities. The texture affects the drainage and the chemical composition of the soil as well as being affected by them. The plant distribution will thus be affected both directly and indirectly by soil texture.

Franseria, *Ephedra*, *Gutierrezia*, *Coleogyne*, and *Krameria* favor coarse soils while *Prosopis*, *Artemisia*, and *Pluchea* favor fine soils (Tables 4, 5, 6, 8, 11, and 12).

INTERACTION BETWEEN FACTORS

The distribution of the various associations will be determined by the interaction of many factors, some of which have been discussed.

The annuals seem not to be confined to given areas to the same extent as perennial plants. The numerous small annuals which bloom in the late winter and early spring require only a shallow soil in which to anchor themselves while utilizing moisture from the winter rains. Most of these annuals are able to grow on every one of the stations examined. There are, however, a few exceptions, which are noted in the descriptions of the several associations. *Bromus rubens* was abundant upon all stations. *Erodium cicutarium*, *Astragalus nuttallianus trichocarpus*, and similar annuals were common at nearly all stations. Only the extremely "alkaline" conditions at Station 13a seemed to provide unfavorable conditions for many of the annual species. The majority of annuals, however, were able to adapt themselves to the great amount of salts present in the soil at Station 14a.

The *Larrea-Franseria* Association, in the area studied, occupies the coarse soils which have a great amount of topsoil particles of granule gravel (Tables 2 and 5). Except for Stations 12, 13c, and 15, this association occupied all the stations with less than 40% of topsoil particles of silt and clay. It must be remembered in this connection that clayey soils.

such as at Station 18, will not dry sift through the 80 mesh sieve, since the particles agglomerate and act as larger particles. Most likely Station 13c could have been occupied by the Larrea-Franseria Association if the soil there had not been so shallow. Station 15 was on a fine sandy loam without gravel or rocks of any sort, located on a nearly level surface but probably not providing sufficient drainage for Franseria. Station 12 did have much Franseria, and perhaps occupies a place transitional between the Larrea and the Larrea-Franseria Associations, but it is placed with the Larrea Association for reasons stated below. The soils of this association are mostly shallow but, if deep, become coarser in texture and in structure with depth (Station 18, Table 2).

Franseria itself is present only on stations with rocky or gravelly, well-drained areas with less than 0.07% sodium sulphate in the surface soil. Parts of the mesa at Station 12 had been partially cleared of brush in the spring of 1939 by a motion picture company for use as an airport. Franseria was common on areas where this removal had occurred. The perennial plant count (Table 6) was taken on part of the cleared region. Where this removal had not taken place, the type of plant cover was more like that at Station 10. All other stations with Franseria have a slope greater than at Station 12.

Lycium andersonii, a plant common in the Larrea-Franseria Association, is able to grow in all soils except those with a very high concentration of sodium sulphate. This plant was rare at Station 14a, where over 5% of sodium sulphate was found in the soil, and it did not occur in soils with higher concentrations, such as at Station 13a.

The Larrea Association was found only on those stations with from 7.6% to 9.6% of granule gravel (Tables 2 and 6). The silt and clay varied from 32.1% to 45.6%. All were located on soils of the Harrisburg stony or gravelly loam types. These soils became somewhat coarser with depth, especially near the ever present "caliche" or hardpan. Station 12, upon which some Franseria was found, had 10% less silt and clay than the other stations of this group, and had about the same amount of silt and clay as the stations of the Larrea-Franseria Association. It did not have the same amount of granule gravel as those stations for there was only 7.6% compared with 19.8% or more for the Larrea-Franseria Association. However, the recent partial clearing of this station, the shallow soil with good drainage, and the location on top of an isolated, high mesa produced a situation favorable for the growth of Franseria patches in an otherwise good stand of Larrea.

Larrea is not present on any station with more than 0.07% sodium sulphate in the surface soil. Where subsoils contain high concentrations of this salt (Stations 7 and 9), creosote-bush is either absent or stunted growths occur sparingly.

The Clistoyucca-Larrea Association is found on rocky soils with 19.8% of granule gravel and with 48.6% silt and clay (Tables 2 and 7). Much coarse

gravel in this soil produces the mixture of fine sandy loam and gravel which lacks many coarse sand particles. The soil texture of this station greatly resembles that upon which the Larrea-Franseria Association is found, except that there is more silt and clay in this soil. Station 9 supported a good growth of Franseria. The Beaverdam Mountains seem to have prevented the Clistoyucca from entering the Saint George Basin to the east, where many stations now supporting Franseria would likely also be able to grow Clistoyucca.

Ephedra nevadensis was found on areas free from sodium sulphate except at Station 9, where there is .06% of sodium sulphate in the subsoil.

The Coleogyne Association occupies shallow soils that are fairly well drained (Tables 2 and 8). Shantz (1938:850) says that Coleogyne occupies soils that are loose, rocky or sandy. In the Saint George area, both Coleogyne and Gutierrezia are common on the type of soil found at Station 13c. The soil texture at this station is more like that where the Larrea-Franseria Association grows than it is like that supporting any other type of association. Undoubtedly, but for the shallowness of the soil, Larrea-Franseria would crowd out most or all of the Gutierrezia and Coleogyne at this station. *Gutierrezia lucida* tolerates traces of sodium sulphate in the soil, but this plant is most abundant where there is good drainage.

The Atriplex-Hilaria Association examined grows upon a topsoil with 11.3% granule gravel and 41.2% silt and clay (Tables 2 and 9). This soil is similar to that supporting the Larrea Association, except that it is deeper and not so gravelly. The drainage is undoubtedly not so good. In this connection it can be noted that near a very small, shallow wash which cuts Station 7 at the west end, a single Larrea plant grows in the gravelly and better drained position.

The Prosopis and the Artemisia filifolia Associations cover stations with less than 3.0% of the soil particles of granule gravel and with an average of 42.4% of silt and clay (Tables 2 and 11). The texture of the soils upon which these associations can grow varies little with depth and the soils are uniformly lacking in coarser particles. The soils are free from "alkali," but Prosopis is probably more resistant than is Artemisia to the effects of these salts. Prosopis is more often found in older, solid-packed soils than is Artemisia, the latter being more or less limited to newly-formed, loose, shifting sands.

The Chrysothamnus Association grows upon soils similar to that supporting the Prosopis Association, but the soil at Station 13b is sandier and contains more granule gravel than the station covered with Prosopis (Table 2). There is also a greater amount of salt in the soil supporting Chrysothamnus Association than that supporting either Prosopis or Artemisia filifolia Associations (Table 3).

The Pluchea Association grows upon fine sandy soil (Tables 2 and 4) that is deep and uniformly mellow. Were it not for the presence of water with the great amount of salt, Station 13a likely could be

covered by either the *Prosopis* or the *Chrysothamnus* Association.

Pluchea sericea occurs where the sulphate concentration varies from 1% to 5%, as at Station 13a (Table 3). The difference in growth habit between *Pluchea* and *Atriplex confertifolia* probably is connected with the water table level, as *Pluchea* is found along watercourses, while extensive dry flats may be covered with *A. confertifolia*. A number of kinds of *Dondia*—both the herbaceous and the semi-woody types—were found on these sulphate-containing soils. This seepweed, as shown by Shantz (1938:852), is an indicator of high "alkali" content and a water table near the surface.

The *Atriplex confertifolia* Association grows on those stations with fine sand that becomes somewhat coarser with depth, until a gypsum-carbonate hardpan is reached (Tables 2 and 10). The presence of "alkali" and the shallowness of the soil probably excludes the *Prosopis* or the *Artemisia filifolia* Associations, while the shallowness of the soil and perhaps the lack of sufficient underground water excludes *Pluchea* Association.

Atriplex confertifolia is confined entirely to stations with sodium sulphate in the soil, although it is not present on all sodium sulphate soils, being replaced by *Pluchea sericea* along watercourses. Shantz (1938:852) pointed out that shade scale indicates the presence of "alkali" within one or two feet of the surface.

The *Clistoyucca-Larrea* Association seems to have been prohibited from entering the Saint George Basin by the barrier of the Beaverdam Mountains. This association is thus confined to the coarse-textured, well-drained, higher slopes of the alluvial fans of the Beaverdam Slope. In the Saint George Basin, the areas with extremely shallow, coarse-textured soils are covered by the *Coleogyne* Association, but support the *Larrea-Franseria* Association where the soil is deeper. On the more nearly level areas the coarse-textured soils of medium depth are favored by the *Larrea* Association unless the soils are deep and small amounts of salts are present in the subsoil, when the *Atriplex-Hilaria* Association covers the area. The fine-textured, "alkaline," deep soils along watercourses support either the *Pluchea* or the *Chrysothamnus* Association, probably depending upon the degree of salinity. The non-"alkaline," deep soils are covered either by *Prosopis* or *Artemisia filifolia* Association, depending upon the soil water level and the soil texture. *Atriplex confertifolia* Association grows upon the shallow, saline soils.

The ultimate distribution of these dominant plants and their associates, then, will depend upon the interaction of many factors. Each of these factors produces an effect upon each of the other factors. As has been shown, gradient affects the slope exposure, the soil texture, the soil depth, the chemical composition of the soil, and the amount of soil water. The variation in soil texture caused by variations in gradient and in parent materials will in turn affect the amount of soil water and the chemical composition

of the soil. The amount of weathering of the soil is influenced by the location and depth of that soil as well as by the drainage. This again affects the chemical composition of the soil, which in turn helps to determine soil texture. In the area studied, the local distribution of the plants is thus determined by the interaction of these many factors.

DISTRIBUTION OF THE MAMMALS

LOCAL RACES OF MAMMALS IN THE SAINT GEORGE AREA

Several local races of mammals are found in the Saint George Basin. For the most part, these races differ from those found west of the Beaverdam Mountains. A number of workers have pointed out color peculiarities in forms from one or the other side of these mountains and not a few have proposed subspecific names that are based mostly upon pelage color differences.

Dark coloration in *Neotoma* from Saint George was reported by Goldman (1910:77). He later named a dark-colored race *N. lepida monstabilis* and assigned lava bed specimens from Mount Trumbull in Arizona and similarly dark-colored animals from Saint George to this race (Goldman 1932:62). The light-colored animals west of the Beaverdam Mountains are *N. l. lepida*.

Dark coloration in some *Peromyscus crinitus* from Saint George was reported by Hardy (1941:90). The animals from the lava ridge (Station 11) that were lightest in color were about the same shade as topotypes of the dark-colored race *P. c. crinitus*. The darkest individuals from Saint George were much darker than typical *crinitus*. In their more recent revision of this species, Hall and Hoffmeister (1942:59), on the basis of cranial and other characters, assign the intergrading animals from the Saint George Basin to *P. c. stephensi*. The specimens from the Beaverdam Slope resemble the light-colored animals from the Saint George area.

The type locality for *Perognathus formosus formosus* is at Saint George. A small series of *P. formosus* skins from Saint George and from the Beaverdam Slope were compared with the type specimens in the United States National Museum by Dr. Remington Kellogg. He stated (letter of July 3, 1942) that specimens from the Beaverdam Slope were indistinguishable from *P. f. mohavensis*. He classed all specimens from the Saint George Basin as *P. f. formosus*, naming a dark skin from the lava rocks (No. 1424b, male, writer's collection) as being essentially a duplicate of the type specimen in color.

Some specimens of Merriam kangaroo-rat from the Saint George Basin are indistinguishable from topotypes of *Dipodomys merriami vulcani*. This is particularly true of animals taken near the lava rocks. The whole series is not typical of this race, but until the various forms of this species are thoroughly understood, it seems best to refer them all to *D. m. vulcani*. The name *D. m. frenatus* proposed by Bole (1936:1) and used by Long (1940:176) is clearly not

available since it is antedated by *D. m. vulcani* of Benson (1934:181) as pointed out by Presnall and Hall (1936:211). The light-colored kangaroo-rats of this species from west of the Beaverdam Mountains are here referred to *D. m. merriami* even though they are much lighter in color than most specimens known as *merriami*, being very near in color to *D. m. similis*, a non-adjacent race from much farther south.

The type locality of *Dipodomys microps celsus* is in Arizona south of and in the same valley as Saint George. This animal is found on soils of reddish color near Saint George and the animals are uniformly darker than the animals taken from the light-colored soils of the Beaverdam Slope. The differences in color, coupled with other characteristics, were so constant that the writer (Hardy 1942:87) proposed the name *Dipodomys microps woodburyi* for the light-colored race of the Beaverdam Slope. The rocky areas of the Beaverdam Mountains probably cause at least a partial isolation and thus serve to maintain the separate identity of these two populations. Specimens which seem to represent intergrades have been taken near some of the lower passes of this Beaverdam Mountain range.

The type locality for the race *Perognathus longimembris virginis* is at Saint George and so mice of this species are tentatively referred to this race, although examination of more material may show the desirability of synonymizing this name with *P. l. arizonensis*. Huey (1939:55) failed to show any significant difference between *arizonensis* and *virginis*—in fact, according to his description, this race differs from *P. l. panamintinus* in the same way as does *P. l. arizonensis* as previously described by Goldman (1931:134). Lack of comparative material prevents a determination of the way in which the Virgin Valley specimens differ in color from the other members of this species. However, Hall (1941a:55) recognized both *arizonensis* and *virginis* in his recent paper.

The Saint George Basin is the center of differentiation for six races of small rodents, while three other forms described from nearby areas have a large part of their range in this basin.

COMPARATIVE ABUNDANCE OF SPECIES

In order to ascertain the comparative numbers of the several kinds of rodents in the region, two trap lines, one of dead traps and one of live traps, were set at each station in the manner explained earlier in this paper. Mammals taken in the live traps on the third night were nearly always those previously marked, so three nights was considered long enough to obtain the majority of mammals that have ranges in the area of each trap line. Since the two trap lines did not differ significantly in the proportion and kind of rodents caught, the results of the two are combined in Table 14.

The asterisks (*) in Table 14 indicate the presence of a species at that station at some trapping period other than that during which this index of abundance was obtained. Usually this record consists of but a

single specimen taken during some other season of the year.

Inasmuch as *Thomomys* requires a type of trap different from other rodents, its presence was determined from fresh gopher diggings and indicated in the table by "x." *Neotoma*, a larger rodent, was not caught readily in these small traps. Except for these two genera, the several species listed in this table should be fairly comparable as to abundance.

TABLE 14. Number of small nocturnal mammals taken in seventy traps during three nights at fifteen stations in the Saint George, Utah, area.

Soil group	I Rocky soils						II Grav- elly soils		III Fine soils							Total
	11	18	8	13c	10	12	16	9	7	14a	14b	13a	13b	17	15	
Station . . .	11	18	8	13c	10	12	16	9	7	14a	14b	13a	13b	17	15	Total
<i>Dipodomys microps</i> . . .							3	14	8	18	17					60
<i>Dipodomys merriami</i> . . .			3		4	9	9	6	7		1	6	3	7	26	81
<i>Perognathus formosus</i> . . .	41	14	5	8	1	6	1	5	8			1	1			91
<i>Perognathus longimembris</i> . . .					10	8	6			11	16				1	52
<i>Peromyscus crinitus</i> . . .	4	1	2	1	1	2	*	*								11
<i>Peromyscus eremicus</i> . . .	*		3	1			1		*			8	*			13
<i>Peromyscus maniculatus</i> . . .									2			1				3
<i>Onychomys torridus</i> . . .							1	5							*	6
<i>Neotoma lepida</i> . . .	5		2	1			2	*	1						1	12
<i>Reithrodontomys megalotis</i> . . .												*		2	*	2
<i>Mus musculus</i> . . .	*	1														1
<i>Thomomys bottae</i> . . .										x	x	x	x	x	x	
Total	50	16	15	11	16	25	21	27	31	29	34	16	4	9	28	332

LOCAL DISTRIBUTION OF CERTAIN SPECIES

The distribution of each race of mammal is determined by the combined effect of numerous factors. The effect of some of these individual factors upon each of the races living in the area is here described.

Dipodomys microps was found only on the gravelly soils of group II and on the fine soils of group III, being excluded from the rocky soils of group I (Table 14). This species occurred only where more than 40% of the soil particles were of silt and clay. Except at Station 7, these soils were shallow and usually contained some sodium sulphate, although occasionally this was present only in the subsoil. However, *microps* may have been prohibited from living in the Harrisburg soils at Stations 10 and 12 because the soils were too shallow, although the animals do live in a similar, less rocky, slightly deeper Harrisburg soil at Station 16.

Dipodomys microps did not occur on the deepest soils, except at Station 7. Perhaps this kangaroo-rat did not live in deep sandy soils because such

areas supported a heavy growth of the *Artemisia*, the *Prosopis*, or the *Pluchea* Associations. The plant cover at Station 7 consisted chiefly of grasses and similar small plants. Station 16 where this animal occurred did have large plants (*Larrea*) but they were spaced distantly from one another (Table 6).

"*Microps*, although widely distributed, does not live as far out on alkaline land toward, for example, a true salt flat devoid of vegetation, as does *Dipodomys merriami*," according to Hall and Dale (1939:47). Examination of the data in the tables on plant distribution and size previously given, as well as of Tables 3 and 14 show that for the stations examined in this area, the reverse is true, *microps* favoring the areas with scanty plant cover and saline concentrations in the soil. This species was not found on steep slopes as it occurred only on areas with a gradient less than 8.3%.

The mounds of *Dipodomys microps* were usually placed at bases of particularly thorny plants. At Station 16, although the spiny *Lycium andersonii* were less numerous than *Larrea*, over half of the mounds noted were located at the bases of *Lycium* plants. It is unknown whether the great number of spines of these plants offered some protection to the animals or whether the seedy berries of the *Lycium* attract them. The roots of these plants may aid in supporting the numerous connecting tunnels of the kangaroo-rat mound.

Perhaps gritty soils are avoided by *Dipodomys microps* more than are the softer feeling soils, either because of the difficulty of digging or because of the need for dust baths. The grittier, granular particles of the newly formed soils might possibly cave into the numerous horizontal tunnels of a *D. microps* mound, whereas these particles might not be so likely to fill a more vertically dug, single tunnel excavated by a smaller rodent. Saint George fine sand (Stations 13a, 13b, and 17) and Tobler fine sandy loam (Station 15) are soils of recent origin (Youngs 1942:64). When compared with the older soils of Stations 7, 9, 14a, 14b, and 16, they feel much more gritty than do the sands of these latter stations. Microscopic examination reveals that these recent soils have a greater proportion of large, red crystalline particles in relation to the fine powdered material than do the older soils. This is especially noticeable in soil from Station 15. Judging from the mammals trapped at this latter station, the total effect of the factors in the closely spaced, tall plant growth on stations with deep, recently formed, gritty soils is such that the habitat seems not to be so favorable for *D. microps* as it is for *Dipodomys merriami*.

The kangaroo-rat *Dipodomys microps* (subspecies *celsus* and *woodburyi*), in the region studied, is an animal which lives under certain definite limiting soil conditions. Soils upon which they abound are those which are older, less gritty, and which lack or have but few large rocks, and may or may not contain granule gravel. These soils are not usually found on steep places, are usually shallow although not ex-

tremely so and are more or less saline in nature, supporting plant types with a low-growing, widely-spaced arrangement.

Dipodomys merriami vulcani is more widespread in these associations than is *Dipodomys microps celsus*. It is found on a greater variety of soils and of plant cover than the latter and is found on steeper slopes. The three specimens taken at Station 8 (Table 14) were obtained near the bottom of the hill where the slope was slightly less than the 19.2% general for this area. The holes, which are smaller than those of *Dipodomys microps*, were noted at the bases of creosote-bushes near the bottom of this hill. Grinnell (1914:242) reported that *D. merriami* is not as restricted in its distribution as *Dipodomys deserti*, because the first-named, smaller animal does not require anywhere near the depth of workable soil as *D. deserti* needs and hence *D. merriami* can occupy more shallow soils. This seems to be true to a lesser extent when *D. merriami* is compared with the larger *D. microps*.

Dipodomys merriami vulcani is most abundant on areas where large plants such as *Artemisia* and *Larrea* are widely spaced, but lives on all but the most gravelly soils (Tables 2 and 14) and variations in plant cover apparently affect it less than they do *Dipodomys microps celsus*. This great tolerance in habitat undoubtedly accounts for the widespread local distribution of *D. m. vulcani*. *Dipodomys merriami merriami* west of the Beaverdam Mountains was found on similar gravelly soil where *Larrea* and *Clistoyucca* are widely spaced.

The distribution of *Perognathus formosus* seems to be correlated with that of rocks and of gravelly soil. The two specimens taken at Stations 13a and 13b (Table 14) were obtained less than 200 feet from nearby rocky hillsides. The specimens taken at Station 7 occurred mostly at the western end of this area, where small rocks and gravel were most abundant. All *P. formosus* specimens came from rocky areas, where they are abundant, or from gravelly soils, where they are common. Long (1940:176) reported trapping this species in rocky areas at Saint George. This pocket-mouse evidently is partial to steep slopes and rock piles. No relationship between the distribution of this mouse and the salinity of the soil, either directly or indirectly through the plants, was discovered. The mouse was not taken on stations with salt concentrations of great value, but such absence may have been due to the absence of rock piles in such situations. These statements apply equally well to both races: *formosus* from the Saint George Basin and *mohavensis* from the Beaverdam Slope.

Perognathus longimembris virginis is resident only on stations where there is less than 10% of the topsoil particles of granule gravel. Stations 7 and 9 had more granule gravel than this, which may explain the absence of this pocket-mouse from such localities. The scanty plant cover at Station 7 and the gradient at Station 9 could also influence the distribution of this animal. This rodent was not found on the sandy, non-firm packing soils of the *Prosopis*

or the *Pluchea* associations. However, a few were recorded from sandy soils of the *Artemisia* Association at Station 15. The soil at this station, Tobler fine sandy loam, is different from the Saint George fine sand at Stations 13a, 13b, and 17. Controlling factors, other than those mentioned, which may influence the distribution of this small pocket-mouse, are unknown at this time.

Peromyscus crinitus occurred on all stations where rocks were present. The only specimen ever taken at Station 16 and also the single individual taken at Station 7 were both trapped less than 200 feet from a rocky hill. This animal is probably nowhere as abundant as are the heteromyids, but a few individuals can nearly always be obtained at each rock pile. No other relationships between this canyon-mouse and either the soil or the plants growing upon the various types of soils can be established from the data accumulated.

Peromyscus eremicus seems to be able to build its home either in rock piles or in the softer, sandy soils. A number were taken near holes at the roots of *Atriplex lentiformis* and *Pluchea sericea* at Station 13a. Long (1940:178) reported that they were "abundant in the rich loamy soils of the river bottom, but were not taken in rocky places." They are most common in the sandy soils, but are less frequently obtained in rock piles. A few of those listed in Table 14 from such rocky hillside stations as 8 and 13c could be wanderers from the nearby Station 13a, but the specimen taken at Station 11 and other individuals trapped in similar rocky areas can hardly be accounted for in this way. However, it does seem that *P. eremicus* is primarily an inhabitant of sandy soils where the vegetation is heavy.

The pocket-gopher (*Thomomys bottae nicholi*) does not occur in rocky or gravelly soils and it is limited to those areas with less than 3% granule gravel. It did not dig on steep hillsides in the area studied. This pocket-gopher seemingly is not influenced in its distribution by the salinity of the soil, since it was found in even the most saline areas. This is similar to the findings of Davis, Ramsey & Arendale (1938:416) with respect to the pocket-gophers of the genus *Geomys* in Texas. They found that the pH value of the soil had no effect upon the distribution of these pocket-gophers. Pocket-gophers were found to be "just as successful in very acid soil as they are in neutral or basic soils." Dixon (1922:144) said that "gophers prefer to work in sandy soil. Hard or 'tight' ground is avoided." Phillips (1936:677) says that in Oklahoma "It is possible that the greater imperviousness of soils in heavily overgrazed areas is both cause and result of the absence of pocket-gophers."

The other kinds of small rodents were taken in numbers too few to justify statements about the factors controlling their habitats. Except for three specimens of *Onychomys torridus longicaudus* from Station 15, these scorpion-mice were found on gravelly soils (Stations 7 and 9). These are the only two stations at which winter fat (*Eurotia lanata*) was

found. This, however, is possibly only a coincidence.

All four specimens of *Mus* were from rocky situations. Here again, however, the numbers involved are too few to allow a statement that in the field this species is at all restricted to this type of habitat.

The desert harvest-mouse (*Reithrodontomys megalotis megalotis*) is known to nest in cattails and similar heavy plant cover, where it builds its nest above the base of the heavy vegetation. Long (1940:177) reported that these animals favored habitats in the vicinity of water, although he took them in southern Utah "far from water on the driest desert." This species was taken in the *Pluchea*, the *Prosopis*, and the *Artemisia* Associations—the areas with the highest and heaviest growth of plant life (Tables 4, 11, 12, and 14). This is an example of a mammal whose distribution is likely correlated with the presence of fairly heavy vegetation.

The woodrats (*Neotoma lepida lepida* and *N. l. monstabilis*) because of their larger size, possibly may be able to move greater distances than the smaller forms. *N. l. monstabilis* is often taken some distance from its favorite rock pile (Stations 7 and 15). *N. l. lepida* is known to build nests in yucca clumps and in the sides of tortoise dens at Station 9. Thus the character of the soil seems not to restrict these adaptable rodents to comparatively small areas as it does some of the smaller forms.

The degree of mobility certainly affects the distribution of animals although species with greater power of travel may, by reason of sparse number, occupy only the most favorable dwelling places. Bats are able to fly over all areas seeking food, but only five of the eleven species collected are known to remain beneath rocks during the day. Others probably seek trees, buildings, or similar situations for their quietest periods.

The two species of rabbits (*Sylvilagus auduboni arizonae* and *Lepus californicus deserticola*), being able to wander widely (Orr 1940:6), were observed at nearly all stations, but were most numerous at such stations (9, 13a, 15) as offered thick plant cover for shelter. Near Station 9, both species favored the *Emplectocladus* Association, where they sought safety either in the large clumps of desert almond or in the winter dens of the desert tortoise. *Lepus* usually takes refuge in flight although it has been seen at least twice to enter tortoise dens. *Sylvilagus* is commonly found in these dens.

The distribution of the rock-squirrel (*Citellus variegatus grammurus*) as the name implies, is well correlated with rock piles. The species is rarely found far from this habitat. This is similar to the condition reported by Burt (1934:404) for this species in southern Nevada. The antelope ground-squirrel (*Citellus leucurus leucurus*) is able to make its home in many situations and it lives in rock piles as well as along sandy washes. During 1939 and 1940 this species was abundant, thus repeating the condition reported by Long (1940:174) during 1936. The numbers had seemingly greatly declined by the

spring of 1941, the cause of the decline being unknown.

Carnivores are able to move still more widely than the rodents and hence are probably not so dependent upon soil conditions, although many forms are known to dig burrows. Spotted skunks, foxes, and ring-tailed cats favor rocky hillsides or washes for their dens—at least they were more often seen or taken in such situations.

The greatest total population of small rodents was found at Station 11 (Table 14) where many rocks provided more abundant shelter than was found at any other station. The smallest number lived at 13b where the plants were tall, widely spaced, and there were no rocks. Perhaps the seemingly greater number of carnivores around rock piles is due to this abundance of food near favorable homesites.

FACTORS THAT INFLUENCE LOCAL MAMMALIAN DISTRIBUTION

The distribution of a species of animal is determined by the interaction of numerous factors even though some one particular factor may limit the distribution in a given direction. As Burt (1938:10) has pointed out the "factors that control mammalian distribution in space and time must be looked for in the various components that go to make up the environment. The factors vary in degree of importance, and it is, therefore, difficult . . . always to pick out those which are critical for a given species." It may be of value to examine various factors limiting the distribution of certain forms studied in the present survey.

CLIMATES

"Moisture, in the form of precipitation, affects the distribution of mammals indirectly through its influence on the vegetation and soil" (Burt 1938:11). The amount of precipitation will not vary appreciably between these different stations since all but one are within a three mile radius of Saint George. "Temperature . . . is influential chiefly as it affects the vegetation of an area. . . . Different slope exposures with slightly different temperatures might shelter different mammal species as a result of different vegetation cover" (Burt 1938:11). There seems to be no difference in vegetation cover on different slopes in the Saint George area which can be attributed directly to the effect of slope exposure. As pointed out previously, north and south slopes more often than not are covered with the same plant association. Thus such small temperature differences between various stations which may exist will not likely be critical in determining the presence of any mammalian species at one of these stations and not at the other. Likely any differences in microclimates of these field stations will more likely be caused by differences in soils than by any macroclimatic differences which could exist. The general climate of the area, or macroclimate, will thus be an important but not a critical factor in determining the local distribution of mammalian species on these stations in the Saint George area.

VEGETATION

Vegetation is important as a factor in influencing mammalian distribution chiefly because the plants furnish shelter and food. Plants may be utilized as shelter sites or their vegetative parts may serve as nest material. The woodrat frequently beds his home with parts of *Opuntia*, the prickly pears perhaps offering a measure of protection from marauding forms. Various plant fibers are used in construction of the nest where both old and young find seclusion.

The spacing and size of the plants may be important for the survival of many kinds of mammals. The varying distances between sheltering thorn clumps may mean the difference between life and death in the split-second flight of a rodent from a predator. The role in the life of animals played by the height of plants is not well known, but *Reithrodontomys megalotis megalotis* was almost always found in high and thick vegetation. Plant associations such as the *Atriplex confertifolia* Association offer no natural perching places for birds of prey as do the *Clistoyucca-Larrea* or the *Prosopis* Associations. While these factors may not in and of themselves be determining factors in the distribution of any form, yet they undoubtedly have an influence on the local abundance of rodents.

Heavy plant cover, on the other hand, seems not to be favored by most of the heteromyid rodents. If found in such areas at all, they are never abundant (Stations 13b and 17; Table 14). On the contrary, if the plants are few and widely spaced, the area is not thickly populated by these rodents.

Desert vegetation sends numerous roots through the soil near the surface. These undoubtedly help at times to support the tops or sides of rodent burrows constructed in fine soils. The roots of *Lycium* have been observed performing this function in the burrows of *Dipodomys microps celsus* at Station 16.

The effect of vegetation in helping to hold soil moisture and to provide humus to the soil is well known. These factors seem to be of less importance in desert areas than in more humid sections where there is a dense vegetation. The plants also help in soil fragmentation. Undoubtedly, however, their most important influence on the mammals is in providing food and shelter.

FOOD

Food is undoubtedly often a limiting factor in the distribution of mammals (Grinnell 1928:433). However, most mammals when living in the proper type of plant association are able to find a few species of plants upon which they may feed, as Dice (1931:312) has pointed out. Food supply was eliminated as a critical factor in the distribution of *Peromyscus* in certain California areas by Grinnell & Orr (1934:211) and in the vicinity of College Station, Texas, Davis, Ramsey & Arendale (1938:416) noted that *Geomys* was not limited in its distribution by the occurrence of a particular kind of plant or group of plants.

The stations studied are all similar in their food production. With the exception of one located in a riparian association (13a), they are of the upland desert type. The small annual plants which probably provide the bulk of food for most rodent forms, are everywhere nearly equally abundant. It is believed that in the area studied, food will not be a factor limiting a species to certain upland stations and excluding it from others. This can be shown more easily for the genus *Dipodomys* than for most other forms.

The food of heteromyid rodents can often be determined from examination of cheek pouches and storage piles. In the area studied, all five races of Heteromyidae have been found with cheek pouches filled with the seeds of various species of *Lepidium* as well as the seeds of *Bromus*, *Larrea*, and *Erodium*. In the spring, the green leaves and blossoms of the last-named plant forms a common food of *Dipodomys*.

Wherever *Dipodomys microps* was trapped, numerous entrances to large mounds occur, but where only *Dipodomys merriami* was found (Stations 8 and 15), this type of mound did not occur. Moore (1930:88) trapped four kangaroo-rats near Saint George and reported these mounds as belonging to *Dipodomys merriami*. Grinnell (1914:242) states that "The burrows of *D. merriami* are not easy to locate, as the entrances are left smoothly closed during the day." The distribution of the large mounds in relation to the distribution of *D. microps* and the fact that when individuals of this species of kangaroo-rat were released they immediately entered holes in these large mounds near which they had been trapped, suggested that these dens are those of *D. microps*.

A visit was made to Station 9 on the Beaverdam Slope on August 19, 1941, about two days after a particularly heavy thunderstorm. Mud had recently been dug from many burrows of these kangaroo-rat mounds. Upon the top of many *Dipodomys microps* homes, usually at the base of a *Larrea* or a *Lycium* shrub, were piled heaps of damp, moldy seeds. A trail strewn with many other seeds showed definitely that each pile had been brought from the underground tunnels. Recent stirring of parts of these piles seemed to indicate that some moving of the seeds had been done, possibly to expose the lower damp layers to the sunlight.

On these *Dipodomys microps* mounds, each kind of seed was piled separately, although the different kinds were piled close together. Usually no more than two to four kinds of seeds were present. The largest heap was usually *Bromus rubens*, all but one pile containing seeds of this species. Two dens had only piles of *B. rubens* seed while one had a pile restricted to *Larrea* seed. The largest pile was estimated at over a gallon. Smaller piles of seed were either of *Larrea*, *Erodium*, *Astragalus nuttallianus trichocarpus*, or *Lepidium*, the last named being next to *Bromus* the most abundant. Likely the different kinds of seeds were piled separately because they were harvested at separate times.

Bromus rubens is a food found in abundance at all

stations. The other varieties of plants whose seeds were used are common at most stations. The entire crop, or even a major portion of seed produced each year is not consumed by the rodents since enough remains to provide an abundant cover of these annuals the following year.

Abundant food of this type at every station examined suggests that lack of food is probably not the factor limiting the distribution of *Dipodomys* to certain stations in this area. Not enough is known concerning the food habits of the other genera of rodents to say whether or not food is a limiting factor, although, inasmuch as they are mostly vegetarian in their food habits, the lack of food of any particular variety of plant is not critical. After laboratory study of the food habits of various eastern forms of the genus *Peromyscus*, Cogshall (1928:221) concluded that "food is probably not an important factor in limiting the habitat distribution of the different species of deer mice." Since food which can be utilized is common at all stations and the climatic factors are fairly uniform over the area, other conditions probably are limiting factors for the various rodents in this area. Howell (1924:53) pointed out that the limiting factor for animal races may be, but is not always, food.

SHELTER

It is a generally accepted fact that small mammals, in order to survive, must have shelter. They must not only have nesting sites to rear offspring and places to which to retire during periods of inactivity, but also must have emergency shelters to which they can flee to escape enemies. Often such shelters may be the limiting factor in the distribution of a land dwelling vertebrate animal (Grinnell 1928:433). The importance of suitable shelters in determining the distribution of various species of *Peromyscus* was pointed out by Grinnell & Orr (1934:211). No correlation was observed between the size of shelters and the distribution of various species of *Peromyscus* in the Saint George Basin. No data, either to support or to disprove the "narrow and broad gauge" shelter theory of Grinnell & Orr, were obtained.

Cover is of more distributional importance than food for the majority of animal races (Howell 1924:53). These shelters may be of various types. In the desert area studied, they may be grouped as shelters in soil, those in and under rocks, and those built in plants.

Plant shelters have been considered above. The number and kinds of shelters in soil and those in and under rocks are determined to a large extent by soil texture.

SOIL TEXTURE

The type of soil may be presumed to affect mammalian distribution in a number of ways. Some species of mammals burrow into the soil while others make their homes in rock fissures or beneath stones. The sand dwellers might have difficulty in hopping through rock piles where there is little or no soil between the closely packed boulders, and, conversely,

rock dwellers would be out of place on a sand dune. Each type of animal is adapted for motility upon a particular type of surface (Dice 1931:313). The presence or absence of dust or fine sand for dusting is probably a fundamental factor in determining the distribution of *Dipodomys* (Dale 1939:711).

Since the various small rodents differ in their digging abilities, weak diggers, such as most kangaroo-rats, will usually be limited to soft soils. Those animals which habitually live underground will thus be limited more or less according to their digging ability in relation to the soil texture.

The texture of the soil has comparatively little effect upon those mammals which live exclusively among or beneath rocks and do not dig. The western bat (*Pipistrellus hesperus hesperus*) hunts food in the Aerial Association but it rests during the day under a rock or in a crevice. Often the roost is beneath a slab or a small rock located in a well-drained spot. The large gray bat (*Antrozous pallidus cantwelli*) was found during the day in cracks of the higher rock ledges.

The long-tailed pocket-mouse (*Perognathus formosus formosus*) was most abundant where the rocks provided shelter, but also is known to dig in gravelly soils. The Kaibab woodrat (*Neotoma lepida monstabilis*) commonly builds its bulky nest of sticks, pebbles and cactus pieces in rock piles, but may also build at the base of clumps of *Yucca* or *Larrea*.

Since soil affects the distribution of plants, it will thus have an indirect effect upon mammalian distribution. Plants often furnish homes as well as emergency shelter, food, and moisture to desert dwelling animals. In many cases, the vegetation type is more important to the mammals than the particular species of plant (Dice 1931:312). The close relationship between heavy plant cover and the distribution of *Reithrodontomys megalotis megalotis* has been pointed out above.

Mammals dig in the soil, build homes both above and below ground, leave their wastes and finally their dead bodies in the soil, all of which ultimately have a profound effect upon the structure of the soil (Taylor 1935:127). Burrowing animals help to form the soil through their digging (Grinnell 1923:144). The combined effects of grazing and burrowing mammals upon the soil may actually produce the plant cover most favorable for them by delaying the development of the climax type of vegetation (Formosov 1928:459). Desert rodents change the chemical character of the soil (Greene & Reynard 1932:80) as well as the textural or physical character (Greene & Murphy 1932:362). Thus mammals influence the texture of the soil which in turn influences the distribution of these mammals.

In general, the rodents of the Saint George area are distributed as follows: in rocky areas: *Peromyscus crinitus*, *Peromyscus eremicus*, *Mus musculus*, both races of *Neotoma lepida*, and both races of *Perognathus formosus*; on gravelly soils: *Perognathus longimembris virginis*, *Peromyscus maniculatus sonoriensis*, both races of *P. formosus*, *Onychomys torridus*

longicaudus, and all four races of *Dipodomys*; on fine soils: *P. l. virginis*, *P. m. sonoriensis*, *P. eremicus*, *Reithrodontomys megalotis megalotis*, *Thomomys bottae nicholi*, and all four races of *Dipodomys*.

SOIL CHEMICALS

The chemicals in the soil influence the distribution of the mammals of the area principally through their effect upon the plants. Shallow soils with a high concentration of sodium sulphate are likely to be covered by *Atriplex confertifolia* Association, a type of plant cover which is favored by *Perognathus longimembris virginis* and *Dipodomys microps celsus*. In the area studied, *D. microps* is found on the saline flats much more frequently than is *Dipodomys merriami*.

If the sulphate-containing soil is deep and with moderate amounts of soil moisture, the resulting *Pluchea* Association will provide homes for *Reithrodontomys megalotis megalotis*. However, heavy vegetation also is found on deep soils with less sulphate, such as the *Prosopis* at Station 17, which also offered shelter to *R. m. megalotis*. No rodents were digging where the sulphate forms a cement-like crust upon the surface although this habitat seemed otherwise suitable for *Dipodomys merriami* (Station 13a).

The most noticeable effect of the carbonates upon the mammals is in the formation of a "caliche." If this hardpan is near the surface, the Merriam kangaroo-rat (*Dipodomys merriami vulcani*) may be present because it is able to live in shallow soils (Stations 8, 10, and 12) whereas the larger Virgin Valley kangaroo-rat (*Dipodomys microps celsus*) is unable to live in such soils. The presence of this hardpan also helps to determine the kind of vegetation that will be present, for the *Prosopis*, the *Artemisia*, or the *Pluchea* Associations did not occur on shallow soils. Animals such as the desert harvest-mouse (*Reithrodontomys megalotis megalotis*) would thus not find sufficient vegetation for shelter on the shallow soils where the carbonates form a hardpan.

The principal effect of these chemicals is thus an indirect one, acting through the plant life to influence the mammals. The principal direct effect is to be found where chemicals form hard crusts either at the surface or below the surface and thus influence the distribution of kangaroo-rats and pocket-mice.

SOIL MOISTURE

The exact amount of soil moisture at the various stations was not measured, but since all of these stations are in desert areas, it is believed that even the riparian association at Station 13a is nearly always dry enough to allow rodents to dig homes in the soil. Most likely the chief influence of the soil moisture on the distribution of mammals at the stations studied will be through its effect upon the type of vegetation supported by the soil and its moisture. The stream-side *Pluchea* Association with its heavy plant growth offered shelter to the Merriam kangaroo-rat (*Dipodomys merriami vulcani*) and the cactus-mouse (*Peromyscus eremicus eremicus*). The latter species was more abundant at 13a than at any other station.

Soil water is also important in that it brings salts to the surface and evaporates leaving a crust of these "alkaline" materials which affects mammalian distribution as shown above.

SOIL DEPTH

The depth of the soil can control mammalian distribution because of the homesites which may or may not be available, as shown by Davis, Ramsey, & Arendale (1938:414) for *Geomys*. Extremely shallow soils will likely not be favored by large animals that are able to dig into deeper soils and thus find greater safety. Carnivores and the larger rodents such as rabbits and ground-squirrels can seek shelter in rocks if the soil is uniformly but a few inches in depth. Small mice or kangaroo-rats, on the other hand, could conceivably construct a burrow even in shallow soil. The Merriam kangaroo-rat, as pointed out by Grinnell (1914:242), is able to live in comparatively shallow soils and thus can enter habitats unsuitable for larger species of kangaroo-rats. The presence of carbonates in sufficient concentration to form a "caliche," thus producing a shallow soil accordingly may affect the distribution of such mammals.

A "caliche" was present beneath the Harrisburg stony loam at Stations 10, 12, and 16. The Merriam kangaroo-rat lives at all three stations, but *Dipodomys microps celsus* was found only at Station 16 where the soil was from eight to ten inches deeper than at the other two stations (Table 2).

Shallow soils, when covered with rocks (Station 8, 11, etc.) can support rock-dwelling mammals such as *Neotoma lepida monstabilis*, *Perognathus formosus formosus*, and *Peromyscus crinitus stephensi*, even though excluding forms digging in deeper soil.

The soil depth also affects mammals through the type of plant cover supported. Large plants which are usually favored by the desert harvest-mouse (*Reithrodontomys megalotis megalotis*) are not usually found on extremely shallow soils such as those at Stations 8, 14a, and 14b.

GRADIENT

The gradient seems to influence the distribution of the various species both directly through affecting the type of home to be constructed and indirectly through its effect upon the soil texture (Table 1), chemical content, and plant cover.

The Virgin Valley kangaroo-rat (*Dipodomys microps celsus*) was not taken on areas with a gradient greater than 8.3%. The characteristic mound of this species was not commonly seen on the steep slopes in the area studied. It is possible that an area with a gradient greater than this would be inhabited by this species of kangaroo-rat if the soil were of the type usually occupied by this species. The Merriam kangaroo-rat (*Dipodomys merriami vulcani*) was found on slopes with a gradient of as much as 19.2%, as at Station 8 where it was taken on the areas near the base of the hill.

The long-tailed pocket-mouse (*Perognathus formosus formosus*) was abundant on steep slopes, but was less often found on more nearly level areas. The

Virgin Valley pocket-mouse (*Perognathus longimembris virginis*) was not taken on stations with a gradient greater than 4.1%.

Peromyscus crinitus and *Neotoma lepida* were abundant on steep slopes, but this, as with *Perognathus formosus*, may be a correlation with the more numerous rocks found in such situations. The other less common species trapped (Table 14) were not taken in numbers great enough to make general statements concerning distribution with respect to gradient.

SLOPE EXPOSURE

Slope exposure was not observed to produce any noticeable variation upon the plant cover as between various stations since all were located within a very limited area. It is likely that, since these mammals seek underground shelter during the heat of the day or during inclement weather, the varying effects of such exposure, if any, will likely differ even less with the animals upon different stations than with the plants.

SOIL COLOR

In the Saint George Basin, the rocks vary in color from black through brown, red, and pink to white. The finer soils are mostly of various shades of red and buff, although a few lighter-colored soils also occur. Benson (1933) and Dice and Blossom (1937:106) demonstrated that there is a correlation between pelage color and the color of soils and rocks in Southern Arizona and adjacent regions. Where the animals live on dark lava rocks, a tendency to develop dark-colored races results (Hooper 1941:40). This evidently has happened in the Saint George Basin with species such as *Neotoma lepida*, *Perognathus formosus*, and *Peromyscus crinitus* which dwell in rocky or gravelly situations and come into intimate contact with lava rock.

Neotoma lepida monstabilis in the Saint George Basin seems to confine itself mostly to the rocks, only occasionally building its nest in vegetation. The rocks in this area are mostly red or black in color and *N. l. monstabilis* is a dark-colored race of woodrat. On the Beaverdam Slope, *Neotoma lepida lepida* commonly builds away from rock piles in the Yucca which are found there. The plants, the soil, and the rocks, when present, are usually light in color and *N. l. lepida* is a light-colored race of woodrat.

Only a very few specimens of *Peromyscus eremicus eremicus* were obtained on lava rock in the Saint George region, but these specimens are somewhat darker than those animals from the red soils at Station 13a and those animals from the light-colored soils of the Beaverdam Slope.

Peromyscus crinitus, another rock-dwelling form, varies in color according to the color of rocks on which it lives. The Black Ridge is a comparatively small area and, at the north end, is adjacent but not directly connected with red hills which are rocky. Over half of the canyon-mice taken on the Black Ridge are dark in color while the remainder are of varying lighter shades (Hardy 1941:90). Occasionally an animal from the nearby red hill is dark in color. The

P. crinitus specimens from the light-colored gravels in the Embletoeladus Association of the Beaverdam Slope are uniformly light in color.

Perognathus formosus varies in color depending upon the color of the rocks where the individuals are trapped. Specimens of *P. f. formosus* from the Black Ridge (Stations 10, 11, 12, and 18) are much darker than those taken on light-colored soil (Station 7). A series of these mammals from the stations east of the Beaverdam Mountains are thus almost as varied in color as the rocks from which they come. West of these mountains the animals (*Perognathus formosus mohavensis*) are uniformly light in color, being like those from Station 7 or lighter. The immature individuals show this as well as do the adults. The small series of dark-colored *P. f. formosus* from the lava areas is somewhat more uniform in color than is the series of *Peromyscus crinitus* from the same lava rocks, but a larger series of *P. formosus* possibly would reveal a greater variation.

The large kangaroo-rats (*Dipodomys microps*) are colored according to the color of the usually fine-textured soils upon which they live. The light-colored race *Dipodomys microps woodburyi* lives on the buffy-colored soils of the Beaverdam Slope while the dark-colored *Dipodomys microps celsus* lives on the reddish-colored soils of the Saint George Basin.

The series of *Dipodomys merriami merriami* from the light-colored soils of the Beaverdam Slope is rather uniformly light-colored. That this is not due to bleaching by the "alkali" in the soil can be shown by the fact that animals from the soils with more "alkali" (Station 13a) are dark in color. The series from the Saint George Basin, taken on soils of various red shades is composed of skins much darker in color than those from the western Beaverdam Slope and are here referred to as *Dipodomys merriami vulcani*.

The variation in a series of *Dipodomys merriami* from various textures of soils has been pointed out previously (Grinnell 1922:77). In a study of various races of this species, Davis (1941:194) says that "Apparently coat color in *Dipodomys* is closely associated with edaphic conditions."

There were no important color variations in the very small series of *Onychomys torridus longicaudus*, *Sylvilagus auduboni arizonae*, *Mus musculus*, *Peromyscus maniculatus sonoriensis*, *Reithrodontomys megalotis megalotis*, and *Perognathus longimembris virginis*. The *Onychomys* specimens, except for three immature animals taken on the red soil of Station 15, were all obtained on the light-colored soils of Stations 7 and 9. There was no significant variation in color within the series. A somewhat larger series of *Perognathus l. virginis* was taken, but only from east of the Beaverdam Mountains on soils which were uniform in color and similar to one another. *Reithrodontomys m. megalotis* lives in thick vegetation and hence would not likely vary in color as much as do the other rodents of the area that are inhabitants of soils less thickly covered with plants. This would likely be so because a particular variety of plant will

not vary as much in color as do the soils. Stebler (1939:391) drew attention to the fact that correlation between pelage color and soil color is most close in those habitats where the soils are exposed extensively through the lack of a heavy vegetation cover. Thus those animals living in heavy vegetation should be expected to show less variation than other species living in closer contact with the soil. The series of harvest-mice, which presents no significant variation, is entirely from east of the Beaverdam Mountains.

BARRIERS

An axiom of zoogeography states that an animal will be found in all areas with a favorable habitat if it can get from its place of origin to that habitat and maintain itself there. The importance of the rocky Beaverdam Mountains as a barrier affecting plants has been discussed above. This is an even more noticeable barrier when animal distribution is examined.

The distribution of the desert tortoise (*Gopherus agassizii*) presents a situation similar to that of the Joshua tree as it naturally occurs only west of the Beaverdam Mountains. Individuals released in the desert regions near Saint George, however, have been able to survive for at least a few years.

The northern crested lizard (*Dipsosaurus dorsalis dorsalis*) has been collected (Woodbury & Hardy 1940:205) along the sandy Beaverdam Wash west of the mountains but is unknown in similar habitats east of these mountains. The long-tailed Uta lizard (*Uta graciosa*) is also known only from the Arizona and Nevada areas on the southwest side of these mountains.

The desert night lizard (*Xantusia vigilis*) has been reported from beneath fallen Joshua tree limbs west of the mountains (Storey 1940:135), but, except for a single specimen likely introduced with a load of wood, it is unknown from the Saint George Basin. However, it is possible that this lizard may eventually be found east of the mountains living in the dead stumps of *Yucca baccata* which are found in the Lower Sonoran Life Belt of this region.

Scott's Oriole (*Icterus parisorum*) is found west of these Beaverdam Mountains where it is known to nest in the Joshua trees (Hardy & Higgins 1940:107).

The rocky gorge cut by the Virgin River through these mountains at the Virgin Narrows probably, because the narrow rocky defile prevents the accumulation of river-washed sand, has prevented some of the animals which dig in river sand from entering the Saint George Basin. Goldman (1939:33; 1939a:257) described the stream-bottom living *Perognathus penicillatus sobrinus* from the Virgin River below these narrows, but this species has not been taken, in spite of extensive trapping, in seemingly identical habitats along the river above this point. Howell (1938:186) reported *Citellus tereticaudus tereticaudus* in the Lower Virgin Valley southwest of these mountains, but it is not found east of them. Burt (1934:415), Durrant (1943:404), and others including the writer have taken *Dipodomys deserti deserti* in the sandy

areas along the lower Virgin River or along the Beaverdam Wash. The writer was unable to obtain specimens in similar habitats in the Saint George Basin.

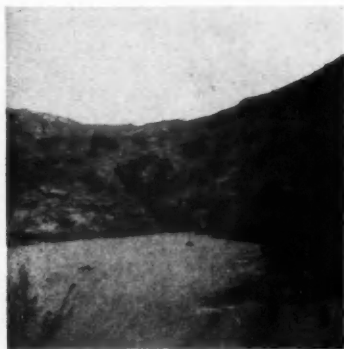


FIG. 19. The Virgin River emerging from the Virgin Narrows. The narrow rocky defile, which is about five miles in length, prevents the accumulation of river-washed sand and thus prevents some of the animals which dig in such sand from entering the Saint George Basin above. At this point in Mohave County, Arizona, the river emerges abruptly from the long, winding, steep-walled chasm.

These animals from west of the Beaverdam Mountains which have not entered the Saint George Basin are either adapted for life in connection with the Joshua tree or live in sandy areas. This mountain range of rocky soils has thus proved itself a barrier to these sand-dwelling and cactus-dwelling forms.

Several forms which have crossed the Beaverdam Mountains or in some way have entered the Saint George Basin, have differentiated in this area so that, as has been previously indicated, they are now best considered as separate races. This range of mountains is the dividing line between the light-colored *Neotoma lepida lepida*, *Perognathus formosus mohavensis*, *Dipodomys merriami merriami*, and *Dipodomys microps woodburyi* on the west and the dark-colored *Neotoma lepida monstabilis*, *Perognathus formosus formosus*, *Dipodomys merriami vulcani*, and *Dipodomys microps celsus* on the east. It also separates *Thomomys bottae virgineus* from the more eastern *Thomomys bottae nicholi*.

The high, steep, lava-strewn slopes of the Black Ridge probably act as an ecological barrier to *Dipodomys microps celsus*. This kangaroo-rat is not found at Stations 10 and 12 upon this mesa and yet it is present at Station 16 on an equally high, but more accessible mesa with slightly deeper and slightly less coarse soil than that upon the Black Ridge. Both *Dipodomys merriami vulcani* and *Perognathus longimembris virginis* live both upon the level benches and the top of the Black Ridge. These two latter species could represent relict populations that have maintained themselves there since the mesa became separated from the surrounding mesas. Or is the soil at Stations 10 and 12 too shallow and coarse

for *D. m. celsus*? The data do not furnish a conclusive answer to this question, but it seems evident that the rock-strewn slopes of the Black Ridge may act as an ecological barrier to *D. m. celsus*.

SPECIATION

Local races of mammals have differentiated in the Saint George Basin. As has been demonstrated, some forms of rodents are adapted for life in rocks and some for life in sandy soils. Some races of small rodents living on the red and black rocks of the Saint George Basin are uniformly darker in color than are the races of small rodents living on the lighter-colored rocks of the Beaverdam Slope. Some forms inhabiting dark-colored soils near Saint George are darker in color than the related forms inhabiting the light-colored soils of the Beaverdam Slope. Mammals living in rocky areas of the Saint George Basin are darker than those of sandy places, possibly because of the adaptation of rock dwellers to life among the black lava rocks.

The dark color of certain specimens of *Peromyscus crinitus* from lava beds (Station 11) has been pointed out previously (Hardy 1941:90). With reference to this species, Hall & Hoffmeister (1942:52) say that "the color of the pelage . . . closely matches the color of the rocks where they live. For example, animals black above, or nearly so, occur among black rocks . . . near Saint George, Utah. Some other areas of dark-colored rocks, nevertheless, are inhabited by canyon mice of a color normal for the surrounding area." This latter condition likely depends upon the fact that the lava area is comparatively small and is located near areas of rocks of other colors. This seems to be similar to the condition of *Perognathus intermedius* at Raven Butte, Arizona (Dice & Blossom 1937:81) and to the coloration noted in a number of small mammals on Valencia County, New Mexico, lava beds by Hooper (1941:40).

Twenty-six specimens of *Peromyscus crinitus* from Saint George, at least seven of which were secured some distance from lava rock as they were taken on the south side of the Virgin River, were examined by Hall & Hoffmeister. They state (page 59) that "At Saint George, Utah, on rocks of a generally reddish color, most mice caught were typical of *stephensi* in color, but one is nearly black. Why some specimens here should be nearly black, others as light as typical *stephensi*, and still others of intermediate shades, we do not know." From the above statement, it is presumed that the material from Saint George examined by Hall & Hoffmeister was not taken from lava rock but from the reddish-colored rocks that are prevalent in the area. As shown elsewhere (Hardy 1941:90) about half of the *P. crinitus* from the lava ridges (Station 11) are dark. Upon the nearby red soils of Station 8, most of the mice are lighter in color and the few dark-colored individuals secured are presumed to be a result of interbreeding with the population of the nearby lava ridges.

Perognathus formosus and *Peromyscus crinitus* are

usually more or less abundant in lava boulder piles. Natural selection is presumed to have played its part here in the adaptation of these forms each to its own particular color of background. Individuals from the lava are dark-colored while those from light-colored rocks are much lighter in color. Isolation is evidently necessary for the differentiation of dark-colored local races as shown by Benson (1933:54) and by Hooper (1941:42). Colonies of these two species of rodents may not have been entirely isolated by the Beaverdam Mountains, since these forms are able to live in rocky situations, and this may cause these forms in the Saint George Basin to be variable in color.

Because specimens of *Perognathus formosus* from lava rocks are more or less uniformly dark, it is desirable to recognize this as a race separate from the uniformly light-colored animals of the Beaverdam Slope. However, the specimens of *Peromyscus crinitus* from the lava areas of Saint George are more variable (Hardy 1941:90) and it is probably not desirable to recognize a local race of this species at this time (Hall & Hoffmeister 1942:51).

The other heteromyid rodents are restricted to sandier soils than is *Perognathus formosus*. *Dipodomys merriami merriami* and *D. m. vulcani* seem able to live in a greater variety of habitats than *Dipodomys microps celus*, *D. m. woodburyi*, or *Perognathus longimembris virginis* and hence come into contact with a greater variety of soils, both as to texture and color. A correlation between lack of subspeciation in *D. merriami* and the numerous types of soil it inhabits was pointed out by Grinnell (1922:77).

In spite of this ability to live in numerous habitats, *Dipodomys merriami* seems to be another example of an animal whose differentiation has been aided by the isolating effect of the Beaverdam Mountains. Animals from west of the mountains live on light-colored soils and, possibly as a result of natural selection, are themselves light in color. Animals from east of the mountains live on soils of various colors, mostly reds and blacks, and they are dark in color, possibly because of the same force of natural selection. The rocky Beaverdam Mountains apparently separate these two local races.

Since the soils upon which the races of *Dipodomys microps* dwell are rather more uniform in texture than those upon which the races of *Dipodomys merriami*, *Perognathus formosus*, or *Peromyscus crinitus* live we should expect less variation in a series of *D. microps* from either side of the mountains than we should expect in either of these latter species. Examination of skins shows this assumption to be true, although the variation in *Dipodomys merriami* is much less than in either *P. formosus* or *P. crinitus*. This is likely correlated with the variety of substrata upon which each is found. *D. merriami* is only infrequently found on lava rock areas and *D. microps* seems to occur there not at all.

The habitat preference of *Dipodomys microps* for the softer feeling, older soils serves to isolate this form into numerous more or less separate populations

which Hall & Dale (1939:47) properly considered as separate races, while the wider-ranging, more tolerant *Dipodomys merriami*, without the same degree of ecological isolation, is not divided into as many races. At first glance this seems to be the opposite effect from that reported by Miller (1942:33) in the case of song sparrows and Lincoln sparrows. He says that the "Establishment of numerous geographically and ecologically isolated colonies of Lincoln sparrows has been thwarted by the rigid adherence to a certain type of fresh-water marsh." The sparrows are able to move from marsh to marsh during migration, but *Dipodomys microps* would not have sufficient motility to move from one favorable soil to another, hence these colonies of kangaroo-rats remain isolated. These findings then support the views of Miller as well as those of Grinnell (1922:77) who reported that there is a distinct relationship between habitat selection and differentiation in *Dipodomys*.

The differentiation of the various races of small mammals of the Saint George Basin has been promoted by a combination of factors. Each mammal is more or less peculiar in its distributional pattern with respect to the distribution of soil type. The soil texture definitely influences this distributional pattern. The various types of soil, furthermore, differ in color. Each species of animal comes, therefore, into contact with different colors of soil, depending upon the texture of the soil in which it lives. Color differentiation of these small rodents thus depends upon both the texture and the color of the soil.

SUMMARY

1. The soils, plants, and mammals of fifteen stations representing ten different ecologic associations of the Lower Sonoran Life Belt of the Mohavian Biotic Province near Saint George, Utah, are described.

2. The texture of the soils in the area studied influences the distribution of small mammals, both directly by the type of shelter offered and indirectly through its effect upon soil chemicals, soil moisture, and vegetation type. Of the eighteen races of rodents studied most intensively in the area, nine commonly inhabit rocky situations; three of these and seven others live in gravelly soils; two rock-living rodents, five inhabitants of gravelly soils, and two others live on fine-textured sands and loams. These eighteen races of rodents seem, therefore, to have varying degrees of dependence upon the texture of the soil.

3. The principal effects of the concentration of soil chemicals on the mammals in this area seems to be through their effect upon the plants. Carbonates which form a hardpan or "caliche" and sulphates which form a cement-like crust upon the surface, however, may interfere with digging by animals and probably directly influence the distribution of such rodents as the kangaroo-rats and pocket-mice.

4. Soil moisture affects the mammalian distribution principally through the effect upon the density of vegetation in this desert area. Nowhere in the area studied was there enough water in the ground to di-

rectly prevent the presence of any of the upland-dwelling rodents.

5. Extremely shallow soils are not used as homesites by burrowing rodents such as *Dipodomys microps* although these areas may be occupied either by the burrowing *Dipodomys merriami* or by rock-dwelling species such as *Peromyscus crinitus* or *Perognathus formosus*. The deeper soils, possibly because of somewhat greater moisture content, affect the mammals indirectly by supporting heavy plant growth and directly by offering room for burrowing.

6. The degree of slope or gradient, perhaps because of varying drainage conditions, has an effect upon the soil chemicals and soil texture, both of which influence mammalian distribution. Some species, such as *Perognathus longimembris virginis* and *Dipodomys microps*, were not taken on steep slopes while *Perognathus formosus* and *Peromyscus crinitus* were most abundant in such situations.

7. Dark-colored soils are most often the homesites of dark-colored races of rodents, while light-colored soils most often offer homesites to light-colored races of rodents.

8. Four species of reptiles and three species of sand-dwelling mammals that live on the light-colored soils west of the rocky Beaverdam Mountains do not enter the Saint George Basin. These mountains also form a barrier which isolates, at least partially, five races of dark-colored mammals on the east of the range from their light-colored relatives west of these mountains.

9. Races which dwell in lava rocks east of the Beaverdam Mountains are usually darker than either the individuals inhabiting the red and brown sands of the Saint George Basin or than their near relatives dwelling in light-colored rocks west of these mountains. This correlation between pelage color and soil color could be a result of selection accompanied by isolation caused by the Beaverdam Mountains.

10. Color differentiation of these small rodents depends upon both the texture and the color of the soil.

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